



Proceedings: Sagebrush Steppe Ecosystems Symposium

**Boise State University
Boise, Idaho
June 21-23, 1999**

Including:

Summary Report:
Snake River Birds of Prey
National Conservation Area
Habitat Restoration Workshop

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Welcome and Plenary Presentation





INTRODUCTORY REMARKS

J. David Brunner

Welcome! For the next two days we will discuss issues surrounding the ecology, uses, and management of sagebrush steppe ecosystems in the western United States, with emphasis on the Great Basin Desert and Columbia Plateau. The goal of this symposium is to identify practical – and I emphasize practical – solutions to stem the tide of loss and improve our abilities to restore sagebrush ecosystems.

BLM has a real interest in the presentations and the knowledge disseminated at this symposium for several reasons:

1) BLM is the largest manager of sagebrush ecosystems in this country and perhaps in the world. Many of our resource values and uses (grazing, watershed function [e.g. clean water], and recreation) are associated with sagebrush rangelands.

2) Sagebrush is a keystone species that is, in part, an indicator of the “health” of the entire region it inhabits. For example, as sagebrush has diminished in cover and area, we have seen sage grouse populations steadily decline until its listing as a threatened or endangered species is now imminent. A local weekly paper in Boise recently commented on this decline and asked the rhetorical question, “Is the sage grouse the next spotted owl?” As land managers, we would all like to turn the sage grouse and sagebrush decline around in order to maintain the flexibility to manage these rangelands for “health” as well as for the multiple uses that our publics expect.

3) The Snake River Birds of Prey National Conservation Area south of Boise is the home of the largest population of nesting raptors in North America. Loss of shrub habitat, especially sagebrush, is one of the most pressing issues in this important wildlife habitat area. In fact, immediately following this symposium, a group of

scientists, managers, and land users will meet for 2 1/2 days to begin developing a strategy to reduce the loss of shrub habitat and restore areas now dominated by cheatgrass, an exotic, highly flammable annual grass.

4) Another reason we must maintain or improve the conditions of our sagebrush rangelands is found in the Idaho Standards for Rangeland Health and Guidelines for Livestock Grazing Management published in August 1997. These Standards and Guidelines, developed by our three public “Resource Advisory Councils” in Idaho, direct our management to restore or maintain “healthy, productive, and diverse native animal habitat and populations of native plants” by implementing proper grazing management practices on our public lands.

5) Finally, noxious weeds are in the forefront of our management today because of their potential to degrade or dominate disturbed sagebrush steppe rangelands. However, we have observed that our drier big sagebrush sites can resist invasion by rush skeletonweed if a good cover of sagebrush is maintained on the site. Once sagebrush is lost through various disturbances, rush skeletonweed is much more apt to invade and eventually dominate these sites. Again, a healthy, intact sagebrush landscape is more resistant to the invasion of at least some noxious weeds.

These are only a few of the reasons why sagebrush steppe ecosystems are valued; we will hear a lot more about them in the next couple of days. I would like to close by first thanking Boise State University for co-sponsoring and hosting this symposium. Our thanks also to the Northwest Chapter of the Society for Ecological Restoration and the USGS’s Forest and Rangeland Ecosystem Science Center for their interest and sponsorship of the symposium.

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SCIENCE, POLITICS AND ECOSYSTEMS: THOUGHTS ON THEIR INTEGRATION

John Freemuth

The move toward an ecosystem-based approach to the management of our public lands must overcome two fundamental problems. One problem could be called the problem of science; the other, the problem of politics. The two problems are related, as perhaps this premise of mine illustrates: science is a necessary but insufficient condition for public decision making.

Let us start with the problem of science. It has certainly become clear that we cannot make effective rangeland policy without solid scientific information – often the laws require it. As a member of the BLM Science Advisory Board, I can tell you that one of our key tasks is figuring out how to get science to the managers who need it most and understanding barriers to the use of science in that bureau. Science can be seen as a problem for a number of reasons. One, there is some confusion about which science should be followed. Looking at our National Forests for a moment, it is equally valid to apply the science of forestry or the science of ecology to pressing management and policy issues. These sciences offer different perspectives, and it is often because they are underpinned by different values. Forestry developed in part with a perspective that looked at forests as tree farms, as places to be wisely managed for the good of society – in this case, for the production of goods and services thought to have economic benefit for large numbers of people. Ecology, on the other hand, tends to look at forests more as “mother earth,” as places to be protected from the ravages of industrial society. Thus, any statements regarding the use of the best science to guide decision makers are rendered problematic at best once we understand the value choices that often lie behind the use of science. Elizabeth Bird put it well when she reminded us:

Should we believe everything the science of ecology has to tell us about our relations with nature? Or should we examine the social construction of ecology itself... and find out if we would want the kind of world that ecology would construct for us if it were to win political hegemony in the sciences?

Mother earth trumps tree farms, as it were.

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Closely tied to this observation is the growing use of what I term “advocacy science.” Advocacy science can take two closely related forms. The first clearly mixes up values and science, where what is a clear value preference ends up masked as a scientific truth. The second works by adopting a certain value preference as a policy goal (logging is harmful) and then attempts to “find the science” that demands a certain conclusion that turns out to be the pre-chosen goal (science tells us that logging harms biodiversity, therefore we must stop logging).

Consider the following example: In the December 1994 issue of *Conservation Biology*, a fascinating editorial was written about the role of conservation biology in range management questions. The opinion piece takes issue with a question asked by Reed Noss, which is whether conservation biologists should “link arms with activists in efforts to reform grazing practices.” The authors’ conclusions are negative. Worried that conservation biologists would damage their credibility by openly advocating political positions, the authors instead suggest asking a different question: “How can livestock grazing be managed to have the fewest impacts on biodiversity and ecosystem integrity?” The authors claim that a special journal symposium on grazing which precipitated their editorial offered no help on this question. Then, in a powerful conclusion to their editorial, we read:

The inherent flaw of deductive reasoning asks one simply to accept that “range management must be dramatically reformed.” How could we continue to conduct this research and attempt to develop valid results if we worked from that premise? Our work as scientists involves recognizing patterns based on data and only then formulating a general rule. More importantly, how can we hope to advance the Society’s mission to preserve biological diversity if our audience of policymakers assumes that we intend to “prove” a presumed conclusion instead of attempting to falsify well-framed null hypotheses?

Finally, public trust in expertise – at least expertise in a general sense – has declined. In our own area of natural resources, the public wonders out loud when it is told that fire is good for the ecosystem after having been told for years by similar people that “only you can prevent forest fires.” They are buffeted by a myriad of



talking heads that talk endlessly to each other about this or that policy topic. Is it any wonder folks turn off their TVs in disgust, convinced that everything causes cancer and that their views are essentially irrelevant to the greatest experts of the day?

THE PROBLEM OF POLITICS

Politics present a different set of problems and issues, which must be understood in order to better manage and protect ecosystems. First, the U.S. political system is designed to check and fragment power; hence, moving in the direction of ecosystem protection takes a good deal of time and effort. Those who advocate for ecosystem protection need to be fully aware of how our current institutional arrangements affect the success of implementing ecosystem protection as a management paradigm. Note, though, that these arrangements are based on assumptions that lead to structuring of political power relationships in a certain way.

There is no better voice here than that of James Madison, who explains one of the key assumptions of the authors of the Constitution this way:

Ambition must be made to counteract ambition.... If men were angels, no government would be necessary. If angels were to govern men, neither external nor internal controls on government would be necessary. In framing a government of men over men, the great difficulty lies in this: you must first enable the government to control the governed and in the next place, oblige it to control itself. A dependence on the people is, no doubt, the primary control on the government, but experience has taught mankind the necessity of auxiliary precautions.

The precautions, of course, are the commonly understood checks and balances, separation of powers, federalism, and republicanism. Power is diffused in the U.S. political system. Policy change is often difficult to achieve.

Madison, in Federalist 10, notes that one of the most important reasons for checking power is the existence of factions (today we would call them interest groups). A faction is “a majority or minority of the whole who are united and actuated by some common impulse of passion, or of interest, adverse to the rights of other citizens or to the permanent and aggregate interests of the community.” Hence, the need to check Madison’s “mischiefs of faction” by representative government, larger political units, and so forth.

Putting all of the above in more modern terms, there is, thus, a designed tendency of the political system to gridlock and for policy shifts to happen rarely. But we do know that we have seen instances where our political system overcame the tendency for political gridlock. One example of particular interest to proponents of

ecosystem management is the development of certain policies during the Progressive Era at the turn of the last century.

Practitioners interested in the implementation of an ecosystem-based management regime would do well to revisit the early days of the Progressive Movement for clues as to how to develop and implement a management regime accepted by an entire society. We remember this era as the time of Gifford Pinchot, Teddy Roosevelt, and the birth of the Conservation Movement. The Progressive Era, of course, institutionalized science-based, expert-centered management as a general approach to the growing complexity of society at the time. For example, the federal bureau that best represented the Progressive Era in land management was the United States Forest Service. Samuel Hays, in his seminal work Conservation and the Gospel of Efficiency, noted that:

Conservationists were led by people who promoted the “rational” use of resources, with a focus on efficiency, planning for future use, and the application of expertise to broad national problems. But they also promoted a system of decision making consistent with that spirit, a process by which the expert would decide in terms of the most efficient dovetailing of all competing resource users according to criteria which were considered to be objective, rational, and above the give-and-take of political conflict.

In the case of the Forest Service, for example, the expertise brought to bear on forest management questions came from the science of forestry.

What is most important about that earlier movement, however, may well be how its themes captured the public imagination. Advocates, as well as students of ecosystem management, should pay close attention to that earlier time. Gifford Pinchot discovered that “in the long run, forestry cannot succeed unless the people who live in and near the forest are for it and not against it.” Pinchot helped lead the effort for professional management of the National Forests. But the key to Pinchot’s success lay not solely in his advocacy of professionalism and expertise, but in the service of both to a democratic vision.

In the words of Bob Pepperman Taylor, “For Pinchot, the conservation of natural resources is of fundamental democratic value because it allows for the possibility of equality of opportunity (access to public resources) for all citizens.” Taylor adds, “If we remove the vision of Progressive democracy from Pinchot’s work, we are left merely with the scientific management and control of nature for no other purpose than brute human survival.”

It is also true that later foresters, as noted by David Clary, “became progressively more narrow in outlook as a result of the kind of specialized education they (Pinchot) encouraged.” The vision may have become



less successful over time because it lost its ability to speak in nonspecialized terms. The point to remember, though, is that early public land management was successful because of its link to a democratic vision accepted by the majority of society at the time, representing an underlying consensus about how a large amount, but not all, of our federal estate should be managed.

The above, however, can be viewed, perhaps, as a road map for the eventual integration of today's science and politics. Today there are a number of newer complications that need consideration as well. The first of those is the increasing use of political appointees at lower levels in the public bureaucracies to move bureau policy in directions sought after by Presidents and other senior officials. The term for this phenomenon is the administrative presidency. Presidents since Richard Nixon have practiced the strategy. Under this strategy, bureaus can be subject to policy shifts from administration to administration, which vary greatly and can cause undue stress on professionals within bureaus.

A second complication concerns the push toward collaborative decision making. What remains unresolved is the role of national versus local groups in terms of representation at the collaborative table. The problem is whether national interests have taken the place of local values, say, in the case of local and national environmental groups. Environmental values may be represented through local groups, but clearly the national groups have their own interests which often lead them to oppose local decision making, even when environmental values are well represented.

Third, internal bureau organization presents interesting political issues too. Many federal bureaus

have dominant professions within them that make up the desired path toward line management positions within the bureau. Any move toward ecosystem management must take into account the sort of management skills needed for the collaborative, cross-jurisdictional approach demanded. The issue should not be whether degrees in ecology (as, say, forestry before) should dominate the line positions but, rather, what skills make for a good ecosystem manager.

Fourth, we must pay close attention to the definition of the problem we are trying to solve. There is no correct way to define a problem, and defining a problem is a political act. Note how, in the symposium program "Welcome," we read about the negative effects of "human encroachment." This is probably true from an observational point of view but also suggests that human encroachment should be curtailed if not reversed. Such a blanket assertion may lead to a good deal of opposition from those who perceive that this will lead to more restrictions on human activity in the name of ecosystem protection.

What is the prescription then? I would suggest that those involved in research, management, and protection of sagebrush ecosystems lay out their vision of why our sagebrush steppe ecosystems are worth our protection. But expect to have an active and involved conversation with those who would like to know more or are in opposition with suggested protection policies that might develop. Science can inform this conversation, but it alone cannot arrive at enforceable goals and purposes for those desert ecosystems. As Wallace Stegner once reminded us: a place is nothing in itself. It has no meaning; it can hardly be said to exist except in terms of human perception, use, and response.

Historical Perspectives in Sagebrush Steppe Ecosystems





SAGEBRUSH SYSTEMATICS AND DISTRIBUTION

E. Durant McArthur

INTRODUCTION

In this paper on sagebrush systematics and distribution, it is appropriate to begin by defining a few terms. Sagebrush, under my definition, are woody North American *Artemisia* of the subgenus *Tridentatae*. *Tridentatae* are one of four subgenera in *Artemisia*. *Tridentatae* or true sagebrush are separated from other *Artemisia* of the subgenera *Artemisia*, *Dracunculus*, and *Seriphidium* (e.g., wormwood, wormseed, sage, tarragon, etc.) by their completely woody nature, exclusive North American distribution, distinctive chemistry and molecular genetics, and their fertile, homogamous, perfect disc flowers (McArthur 1979, McArthur and Sanderson 1999a). There are 11 sagebrush species that, together with their subspecific entities, account for about 20 taxa. *Artemisia* as a whole includes more than 200 species.

We define systematics following Judd et al. (1999): systematics is the science of organismal diversity which entails the discovery, description, and interpretation of biological diversity as well as the synthesis of information in the form of predictive classification systems. According to Judd et al. (1999) the aim of systematics is to discover the branches of the tree of life, to document the changes that have occurred during the evolution of these branches, and to describe taxa (usually species) at the tips of these branches.

Distribution, of course, is the natural geographic range of organisms. For sagebrush taxa, there is a distribution of the whole group and subset distributions of taxa that constitute sagebrush which may be sympatric (occurring in the same area), parapatric (occurring in separate but adjoining areas), and allopatric (occurring in different areas).

SAGEBRUSH SYSTEMATICS

Artemisia is a distinguished name, an etymological descendant of an early Mother Nature. Artemis was the ancient Greek goddess of wild animals, the hunt, and vegetation, and of chastity and childbirth (McArthur 1979). *Tridentatae* and *tridentata* both refer to the characteristic three lobes of many sagebrush taxa.

Subgenus *Tridentatae* of *Artemisia* is a group of plants centered on the landscape-dominant *A. tridentata*

complex. There have been several systematic treatments of the group (see Kornkven et al. 1998 and McArthur et al. 1998a for recent reviews). My colleagues and I (McArthur et al. 1998a, McArthur and Sanderson 1999a) recognize 11 species and 14 subspecies (Table 1). *Artemisia* is centered, in distribution and diversity, on the great Eurasian landmass. There is compelling distributional, chemical, and genetic evidence that North American *Tridentatae* are derived from Eurasian stock and that they differentiated and expanded during Pliocene and Pleistocene with the changing climates and habitats of those epochs (summarized in McArthur et al. 1998a,b; McArthur and Sanderson 1999a).

Differentiation and evolution within *Tridentatae* has been facilitated by polyploidy and hybridization. All the major species (big sagebrush [*A. tridentata*], silver sagebrush [*A. cana*], low sagebrush [*A. arbuscula*], and black sagebrush [*A. nova*]), as well as several less common or more geographically restricted ones (Bigelow sagebrush [*A. bigelovii*] and Rothrock sagebrush [*A. rothrockii*]), include both diploid and polyploid populations (Table 2). Based on habitat occupation, we have hypothesized that polyploidy is adaptive, i.e., polyploid populations are usually found in drier habitats than are related diploids (Sanderson et al. 1989, McArthur and Sanderson 1999a). Polyploids are smaller with slower growth rates that make them better adapted to drier conditions (Sanderson et al. 1989).

Some species have poorer support for taxonomic placement in *Tridentatae* than others. Bigelow sagebrush has floral anomalies, and pygmy sagebrush (*A. pygmaea*) has morphological anomalies; but both have karyotypic and molecular genetic characteristics of *Tridentatae*. There is evidence that sand sage (*A. filifolia*), ordinarily placed in subgenus *Dracunculus*, has some affinities with subgenus *Tridentatae* based on chloroplast DNA, plant chemistry, and chromosomal karyotype (Kornkven et al. 1998, McArthur and Sanderson 1999a). An anomalous plant, *A. palmeri*, is wholly herbaceous but has the floral formula of *Tridentatae*; however, I follow Rydberg (1916) and exclude it from *Tridentatae*.

Hybridization is common in this group and has apparently been a mechanism providing new genetic combinations to facilitate occupation of changing habitats during the evolutionary history of *Tridentatae* (Ward 1953, McArthur et al. 1988, McArthur and Sanderson

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1999a). In a series of studies (reviewed by Graham et al. 1999 and McArthur and Sanderson 1999b), my colleagues and I have examined a narrow hybrid zone between basin (*A. tridentata* ssp. *tridentata*) and mountain (*A. t.* ssp. *vaseyana*) big sagebrush. We have studied adaptation, growth, gene flow, chemistry, physiology, soils, mineral distribution and uptake, and plant and animal communities across the zone and in reciprocally transplanted gardens. We concluded that hybrids are adapted to these zones and that points of contact between differentiated taxa (hybrid zones) could have been the source for differentiation of new genetic combinations. These combinations were able to exploit new habitats associated with changing climates of the Pliocene and Pleistocene Epochs, continuing until the present. Several extant *Tridentatae* species, subspecies, and populations, described and undescribed, are of hybrid origin, e.g., Lahonton low sagebrush (*A. arbuscula* ssp. *longicaulis*), spicate or snowbank big sagebrush (*A. tridentata* ssp. *spiciformis*), and xeric big sagebrush (*A. tridentata* ssp. *xericensis*) (Winward and McArthur 1995, McArthur and Sanderson 1999b). Artificial hybridization may be useful for management purposes in selecting and combining traits in sagebrush for palatability, nutritive quality, and fire tolerance (McArthur et al. 1988, McArthur et al. 1998a).

SAGEBRUSH DISTRIBUTION

Artemisia in general is widely distributed throughout the northern hemisphere with disjunct distribution to some, mainly mountainous, southern hemisphere locations (Good 1974). However, the subgenus *Tridentatae* is wholly western North American (Fig. 1). West of the 100° west longitude at mid-latitudes, sagebrush is a dominant, widely distributed plant (Fig. 1, Table 1). Figure 1 illustrates aspects of the group's distribution, including the wide distribution of the central species, big sagebrush. Big sagebrush, with its subspecies, extends over most of the geographic range covered by the subgenus as a whole. The nature of areas dominated by sagebrush is also illustrated in the figure, using the state of Utah as an example. Large areas are dominated by sagebrush, but some of its species are less significant components of other communities, e.g., mountain brush and pinyon-juniper. However, some taxa, e.g., pygmy

sagebrush, Bigelow sagebrush, Alkali sagebrush (*A. longiloba*), and stiff sagebrush (*A. rigida*), grow in specific, limited habitats.

Sagebrush taxa grow at elevations and precipitation levels above the salt desert shrub communities, i.e., precipitation above 18-20 cm per year. For the common big sagebrush subspecies in the Intermountain area, the annual precipitation levels are: about 32-36 cm for basin big sagebrush (however, basin big sagebrush often grows in areas that benefit from seasonally high water tables at different precipitation levels), about 20-30 cm for Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*), and generally above 30 cm for mountain big sagebrush (Monsen and McArthur 1984, Goodrich et al. 1999).

General distribution and site conditions for each species and subspecies are presented in Table 1. Distribution of sagebrush species and subspecies is usually associated with specific soil properties and soil parental material as well as climatic differences (Passey et al. 1982, Wang et al. 1998, Wang et al. 1999). Seed recruitment conditions are generally tied to local climatic conditions, i.e., seeds germinate and establish better in habitats climatically like those that produced them (Meyer and Monsen 1992).

There is a high incidence of parapatric and sympatric distribution within *Tridentatae*. Many taxa, however, have allopatric distributions with regard to one another (Table 1). This type of distribution pattern, together with wind pollination, facilitates hybridization within the group. However, despite hybridization and the occurrence of hybrid zones, most populations and individuals are clearly assignable to parental taxa (Beetle 1970).

Unfortunately, sagebrush ecosystems have been badly disturbed (intensive grazing, introduction of cheatgrass, etc.) beyond historic natural disturbance cycles, as witnessed by other contributions in this symposium and by previous works, e.g., Passey et al. (1982) and contributions in Monsen and Kitchen (1994). I believe integrity and maintenance of sagebrush communities is important for healthy, naturally functioning ecosystems on a continental scale, as many other components of sagebrush ecosystems are dependent on this keystone species.

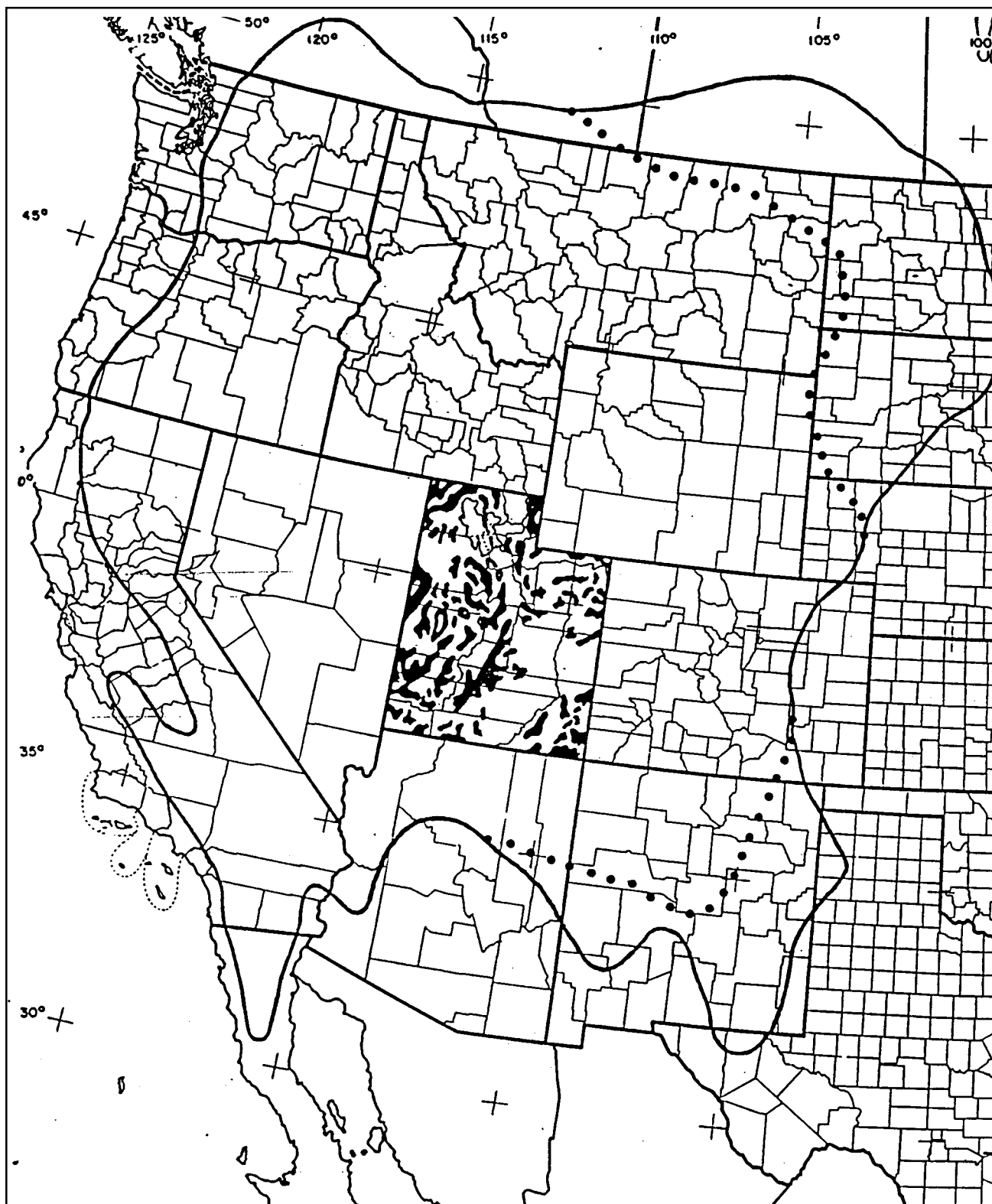


Figure 1. Distribution of sagebrush (subgenus *Tridentatae* of *Artemisia*). Solid line is the extent of distribution. Dotted lines delineate areas where *A. tridentata* doesn't grow; the northeast extension reflects the distribution of *A. cana*, and the southeast extension reflects the distribution of *A. bigelovii*. Solid black areas are zones of sagebrush dominance in Utah (from McArthur 1979).

Table 1. Sagebrush (subgenus *Tridentatae*) taxa (species and subspecies) with their general distributions and site adaptation (after McArthur 1994 with additions from Winward and McArthur 1995 and Welsh and Goodrich 1995).

<u>Species</u>	<u>Subspecies</u>	<u>Distribution and Site Adaptation</u>
Low sagebrush (<i>A. arbuscula</i>)	Low sagebrush (<i>arbuscula</i>)	W. Wyoming to S.C. Washington and N. California on dry, sterile, rocky, shallow, alkaline, clay soils.
	Cleftleaf sagebrush (<i>thermopola</i>)	W. Wyoming, N. Utah, and E. Idaho on spring-flooded, summer-dry soils.
	Lahontan sagebrush (<i>longicaulis</i>)	N.W. Nevada extending into adjacent California and Oregon on soils of low water-holding capacity and shallow depth, usually around and above the old shoreline of Lake Lahontan.
Coaltown sagebrush (<i>A. argillosa</i>)		Jackson County, Colorado, on alkaline spoil material.
Bigelow sagebrush (<i>A. bigelovii</i>)		Four Corners area extending to N.E. Utah, S.E. California, and W. Texas on rocky, sandy soils.
Silver sagebrush (<i>A. cana</i>)	Bolander silver sagebrush (<i>bolanderi</i>)	E. Oregon, W. Nevada, and N. California on alkaline basins.
	Plains silver sagebrush (<i>cana</i>)	Generally E. of Continental Divide, Alberta and Manitoba to Colorado on loamy to sandy soils of river bottoms.
	Mountain silver sagebrush (<i>viscidula</i>)	Generally W. of Continental Divide, Montana and Oregon to Arizona and New Mexico in mountain areas along streams and in areas of heavy snowpack.
Alkali sagebrush (<i>A. longiloba</i>)		S.W. Montana, N.W. Colorado, W. Wyoming, N. Utah, S. Idaho, N. Nevada, and E. Oregon on heavy soils derived from alkaline shales or on lighter, limey soils.
Black sagebrush (<i>A. nova</i>)	Duchesne black sagebrush (<i>duchesnicola</i>) ^a	Uinta Basin, Utah, in reddish clay soil uplands.
	Black sagebrush (<i>nova</i>)	S.E. Oregon and S.C. Montana to S. California and N.W. New Mexico on dry, shallow, stony soils, with some affinity for calcareous conditions.
Pygmy sagebrush (<i>A. pygmaea</i>)		C. Nevada and N.E. Utah to N. Arizona on desert calcareous soils.
Stiff sagebrush (<i>A. rigida</i>)		E. Oregon, E. Washington, and W.C. Idaho on rocky scablands.
Rothrock sagebrush (<i>A. rothrockii</i>)		California and Nevada in deep soils along the forest margins of the Sierra Nevada and outliers.

(Continued)



Table 1 (cont.)

<u>Species</u>	<u>Subspecies</u>	<u>Distribution and Site Adaptation</u>
Big sagebrush (<i>A. tridentata</i>)	Snowbank big sagebrush (<i>spiciformis</i>)	Wyoming, Idaho, Colorado, and Utah in high mountains.
	Basin big sagebrush (<i>tridentata</i>)	British Columbia and Montana to New Mexico and Baja California in dry, deep, well-drained soils on plains, valleys, and foothills.
	Mountain big sagebrush (<i>vaseyana</i>)	British Columbia and Montana to Baja California in dry, deep, well-drained soils on foothills and mountains.
	Wyoming big sagebrush (<i>wyomingensis</i>)	North Dakota and Washington to Arizona and New Mexico in poor shallow soils often underlain by a caliche or silica layer.
	Xeric big sagebrush (<i>xericensis</i>)	W.C. Idaho on basaltic and granitic soils.
Threetip sagebrush (<i>A. tripartita</i>)	Wyoming threetip sagebrush (<i>rupicola</i>)	Wyoming on rocky hills.
	Tall threetip sagebrush (<i>tripartita</i>)	E. Washington and W. Montana to N. Nevada and N. Utah on moderate-to-deep well-drained soils

^aDescribed at the variety level by Welsh and Goodrich (1995) but analogous to the other subspecies listed in the table.

Table 2. Summary of subgenus *Tridentatae* chromosome counts (after McArthur and Sanderson 1999a).

Species	No. <u>ssp.</u> ^a	No. <u>pops.</u>	No. <u>plants</u>	<u>2x</u>	No. pops. ^b at		
					<u>4x</u>	<u>6x</u>	<u>8x</u>
<i>Artemisia arbuscula</i> ^b	2	51	139	25	18	8	0
<i>Artemisia argillosa</i>	1	1	4	0	1	0	0
<i>Artemisia bigelovii</i> ^b	1	12	46	4	7	0	1
<i>Artemisia cana</i>	3	43	96	13	6	0	24
<i>Artemisia longiloba</i>	1	3	8	2	1	0	0
<i>Artemisia nova</i> ^b	1	36	81	13	23	0	0
<i>Artemisia pygmaea</i> ^b	1	4	12	4	0	0	0
<i>Artemisia rigida</i> ^b	1	13	30	8	5	0	0
<i>Artemisia rothrockii</i> ^b	1	7	8	0	2	4	1
<i>Artemisia tridentata</i> ^b	5	427	1103	213	214	0	0
<i>Artemisia tripartita</i> ^b	<u>1</u>	<u>20</u>	<u>46</u>	<u>14</u>	<u>6</u>	<u>0</u>	<u>0</u>
Totals		617	1573	296	283	12	26

^a Includes only ssp. for which chromosome numbers have been determined. There are additional subspecific taxa that are cytologically unknown: *A. arbuscula* ssp. *thermopola*, *A. nova* var. *duchesnicola*, *A. tripartita* ssp. *rupicola*.

^b Some populations have plants at more than one chromosome ploidy level. The ploidy (x) level reported here is that of the mode of the sampled population(s) or the lowest number when an equal number of plants were at different x levels.



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SYNECOLOGY AND DISTURBANCE REGIMES OF SAGEBRUSH STEPPE ECOSYSTEMS

Neil E. West

ABSTRACT

The pre-Columbian mixed-growth form, composition, and structure of sagebrush steppes was mostly due to the highly variable semiarid climate and long fire-free intervals. The weak stability of this relatively complex vegetation was easily upset by excessive livestock grazing, especially in drought periods. After a few decades of uncontrolled livestock grazing, it was easy for introduced winter annuals, especially cheatgrass, to dominate the understory and alter the fire regime to larger, more frequent fires that occur earlier in the year. Accelerated soil erosion has caused many sites to lose the potential for management back toward native perennial dominance by controlling only livestock and fire. Major investments will probably be necessary to lengthen the current fire-free interval, as well as reduce the size of fires and their occurrence during late spring and early summer on large areas of cheatgrass dominance. Livestock could be used in some circumstances to help reverse the damage they did before grazing became regulated. Opportunities to apply genetic engineering to native plants and new herbicides to cheatgrass should also be explored before even more noxious biennials gain a major foothold.

INTRODUCTION

Durant McArthur (this volume) appropriately began by giving us background in sagebrush taxonomy, species distributions, and autecology. I now perceive my role as one of reviewing the synecology of an ecosystem type called "sagebrush steppe." This includes the disturbance regimes intrinsic to this ecosystem.

DEFINITIONS

I have restricted my coverage to the 45 million ha of sagebrush steppe (West 1983a) and alert you to the fact that not all areas currently or recently having vegetation with a woody *Artemisia* dominant are sagebrush steppe, particularly in the drier, less diverse, less productive, less resistant, less resilient sagebrush semi-desert to the south (West 1983b). I am purposely avoiding drawing on information from sagebrush semi-deserts in this paper.

ECOSYSTEM STRUCTURE

Climate - Sagebrush steppe occurs where there has been until recently, or still is, a sharing of dominance between shrub and herbaceous growth forms. The fundamental reason for this is that, on average, continental semiarid climates occur here. More important than the climatic means is the understanding that these climates have high coefficients of variation (~30%) in total annual precipitation, with rapid fluctuation between some more favorable years that promote the shallow, fibrous-rooted, herbaceous plants and droughty years that favor the more deeply rooted shrubs (Fig. 1). Herbaceous plants develop earlier in the growing season and thrive on spring rains, whereas shrubs lag in their phenological development because they can draw from deeply infiltrating moisture from snowmelt the previous fall and winter. While this leads to some compensation between species to produce a dampened yet higher level of production in shrub steppes than in semi-deserts, it also makes these systems much more difficult to understand and sustainably manage than either grassland or desert.

The fire-return interval in the Pre-Columbian condition probably varied between 25 years in wetter areas (Houston 1973) and 110 years on the central Snake River Plains (Whisenant 1990) (Fig. 2). Otherwise, the earliest observers would have called this the rabbitbrush steppe because the shorter-lived and root-sprouting *Chrysothamnus* spp. would have prevailed (Young 1983).

Soils - Soils give us some reflection of long-term climatic and vegetational influences. Most sagebrush steppe soils are Xerolls – that is, the most drought-affected Mollisols – if the surface layers haven't been eroded. Most soils of sagebrush semi-desert are Aridisols (West and Young 2000). Thus, where flora and fauna are highly altered, one can use soil profile characteristics to gauge the potential of sites for recovery through management or restoration.

Vegetation - The floristic diversity of the sagebrush steppe is moderate by regional standards. Daubenmire (1970) found an average of 20 vascular plant species in 1,000-m² plots on relict sites in central Washington. Tisdale et al. (1965) found from 13 to 24 vascular plant species in examples of three community types on an ungrazed site in southern Idaho. Mueggler (1982) found 24 to 41 vascular plant species in a set of 68 lightly

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grazed macroplots in the sagebrush steppe of western Montana.

The vertical and horizontal structure of the sagebrush steppe consists of shrub-dominated and herb-dominated phases (West 1983a). The shrubs usually vary in height from about 0.5 m for either young plants of the tall sagebrushes or mature low-statured species to more than 2 m for the tallest sagebrushes on the best sites. The fraction of ground surface covered by the various growth forms varies greatly depending on site and successional status.

Herbs on relict sagebrush steppe sites are usually perennial hemicryptophytes (Daubenmire 1975). The proportion of geophytes approaches 20%. Bork et al. (1998) claim that grasses are more often situated closer to the shrubs than the forbs. Annuals and microphytes are usually more abundant in the middle of the inter-spaces between shrubs.

The total phytomass standing crop of relictual stands varies between 2 and 12 t/ha, with about half of that occurring below ground. Only about 15% of the above-ground phytomass may be attributable to the current year's growth of shrubs. Above-ground net primary production varies from about 100 to 1,500 kg/ha/yr for relict areas (Passey et al. 1982).

Animals - Native vertebrate animals of the sagebrush steppe are a mixture of grassland and desert species. About 100 bird and 70 mammal species can be found in sagebrush habitats (Braun et al. 1976). Although the vertebrate community is most diverse when the pattern of plant communities is most structurally diverse (Parmenter and MacMahon 1983, Maser et al. 1984), the only tightly co-evolved and thus sagebrush obligate vertebrate species are the sage grouse, sage sparrow, Brewer's sparrow, sage thrasher, pygmy rabbit, sagebrush vole, sagebrush lizard, and pronghorn (Paige and Ritter 1999). While none of these is known to cause major negative feedbacks on the vegetation, jackrabbits can (Young 1994).

Over 1,000 species of insects have been found on example sites (West 1999), more than 76 species on sagebrush alone (Wiens et al. 1991). While some are known to alter the vegetation during occasional population explosions, e.g., *Aroga* moth and cicadas (West 1999), grasshoppers and crickets (Yensen 1980) can do so more regularly. The functional importance of most invertebrates is yet to be discovered.

Microbes - We know very little about what microbes are present and how they influence ecosystem processes within the sagebrush steppe. Hopefully, these organisms and the work they do, mainly decomposition and nutrient cycling, will receive more attention in the future. Global environmental changes are likely to produce some unexpected interactions among plants, microorganisms, and soil degradation (West et al. 1994).

ECOSYSTEM DYNAMICS

We now need to turn to consideration of how the above components interact and how the ecosystem has changed. In order to interweave the historical with the ecological, I will follow the recent example of Rapport and Whitford (1999) in organizing this overview of how sagebrush steppes have responded to stress. I will also tie the changes to a recent model of retrogression in the sagebrush steppe (West 1999). Only the major states and pathways are considered here.

Pristine Conditions (State I)

Pristine ecosystems (State I in Fig. 3) no longer exist, nor are they likely to be recoverable. The reasons for this view are:

1. Humans (indigenous peoples) are no longer hunting, gathering, and burning the areas. The previous fire regimes are no longer in place; and, as the vegetation has changed in response to fires, the hydrologic and nutrient cycles have been altered, as has the habitat for numerous animals and microbes.
2. The present climate is warmer and drier than the cooler, wetter Little Ice Age climate which prevailed from about 1500 to 1890. Thus, only heat- and drought-tolerant species may now thrive under global warming.
3. Atmospheric CO₂ has increased about 20% during the past century, altering the competitive balances in this vegetation as well as changing the nutritional qualities of the phytomass and litter (Polley 1997).
4. About 15% of the flora is new to the region. Since the close of the Pleistocene, extinctions have been minor.

Since we can reverse none of these influences, at least in the short term, we should learn to live with what remains and manage it toward the mix of desired plant communities we choose for each landscape (Paige and Ritter 1999).

Relictual Conditions (State II)

There are some remnants of the present landscapes that have escaped direct human influences. These relicts exist because they have no surface water, are surrounded by difficult topography, or are protected in special-use areas, e.g., Research Natural Areas. I place these in State II (Fig. 3). Passey et al. (1982) describe many examples. These relicts are not completely reliable as reference conditions because they are incomplete ecosystems. They lack indigenous humans as well as normal kinds and numbers of native animals and have usually experienced lengthened fire frequencies because of their isolation. Relicts are further influenced by air pollutants, climatic change, and invasion by exotics (Passey et al. 1982).

Most of the existing late seral sagebrush steppe with good perennial understory (State II in Fig. 3) has had light livestock use, especially earlier in the century when



sheep were very abundant. Even light livestock use (T_1) puts inordinate pressure on a few highly palatable species (“ice cream plants”), partially explaining the lack of a return arrow from State II to State I. I estimate that less than 1% of the region remains in State II (Fig. 4). These shrub steppes with smaller, more scattered shrubs and almost complete perennial herbaceous understories are less susceptible to large-scale fires and subsequent invasion by cheatgrass (Peters and Bunting 1984).

Stagnant Sagebrush (State III)

Because livestock that graze native sagebrush steppe tend to avoid the unpalatable species (usually woody species), shrubs are freed from competition and achieve dominance quickly (10-15 years). With the removal of fine connecting fuels, the chance of fire is also reduced in State III (Fig. 3). About 25% of this ecosystem type is estimated to exist in this state (Fig. 4). In some places, feral horses, protected by law on most public lands, have created and maintain sagebrush stands with little remaining herbaceous perennial understory. Most of these stands can remain stagnant for decades (Rice and Westoby 1978, Sneva et al. 1984, Winward 1991). The dense, competitive stands of excess sagebrush prevent perennial herbaceous species from recovering when grazing is either reduced (T_3) or excluded over very long intervals (Bork et al. 1998).

Herb-dominated Stands (State IV)

Brush-choked or stagnant stands of sagebrush (State III) were usually chosen by both livestock and wildlife managers in the past for manipulation to diversify vegetation structure. Such treatments locally enhance a stand by concentrating livestock use and reducing pressure elsewhere, while simultaneously creating an advantage for some wildlife species through vegetation modifications via grazing systems, prescribed burning, brush-beating, or chaining (T_3). For example, grazing sheep only in the fall – because they consume more sagebrush then but cannot heavily impact the herbs – can help achieve a conversion from State III to State IV and even increase floristic diversity compared to adjacent exclosures ungrazed for decades (Bork et al. 1998). Prescribed burning (Harniss and Murray 1973) can also be applied to stands with sufficient remnant populations of perennial native herbs to quickly recover following brush kill. A rest-rotation grazing system or winter-only use (Mosley 1996) will often allow a slow return (T_6) to State II from State IV.

Reduction of brush also enhances water yields (Sturges 1977), and some seeps, springs, and streams reappear. When phenoxy herbicides are used alone (Evans et al. 1979) (T_4) or in conjunction with fire, the community becomes dominated by native grasses (State IV, Fig. 3) because phenoxy herbicides negatively impact all broad-leaved species. This conversion slowly returns

(T_6) to State II only with conservative grazing. About 5% of the remaining sagebrush steppe is now estimated to be in State IV. This is a short-lived state, especially under heavy grazing (T_5). Mueggler (1982) found enhanced alpha diversity in moderately grazed sagebrush steppe communities in western Montana following prescribed fire, 2,4-D, and brush-beating treatments. Summer fires can damage some grass species (Young 1983) but encourage the resprouting rabbitbrushes (*Chrysothamnus* spp.) and horsebrushes (*Tetradymia* spp.) (Anderson et al. 1996).

The perceived will of a majority of Americans now is to identify remaining areas occupied by States II and III, especially those on public lands, and protect them from development. In other words, I agree with Paige and Ritter (1999) that no net loss of sagebrush should be a regional objective to prevent further declines in biodiversity (West 1999). Some advocate all such areas have livestock removed (Kerr 1994), whereas others (Bock et al. 1993) propose that 25% have livestock excluded. Rose et al. (personal communication) have, however, recently demonstrated that lightly grazed sagebrush steppe has higher species richness than adjacent exclosures dating to 1937. Others propose restoration efforts to bring further-degraded systems back to States I or II. Whether that is possible and economical is discussed in the remainder of this volume.

Regardless of one's view of the matter, State II and III areas will serve as a major “parts catalog” for restoration efforts. The Gap Analysis Program (GAP) of the U.S. Fish and Wildlife Service (Scott et al. 1993) and the various natural heritage programs initiated by the Nature Conservancy are well under way to identify such areas.

I expect to see physical modifications for enhancing production of food and fiber (formerly called range “improvements”) to be more spatially limited than in the past. Such actions on public lands or with public monies on private land require environmental assessments or impact statements and, thus, public scrutiny and debate. The remaining sagebrush-dominated public lands will probably be consciously protected to provide the later seral condition patches necessary to hold a broader spectrum of all species and meet the special requirements for some featured and obligate species (Paige and Ritter 1999).

Rangeland managers in the past strove to reduce the land's limitations for producing livestock. These limitations were mainly topography, forage availability, and water. For example, trails were constructed into areas where topographic breaks limited previous livestock access. Natural water was supplemented by developing springs, building stock tanks and small dams, drilling wells, and piping and hauling water. Fences were constructed and salt distributed to control livestock movement and institute grazing management systems (e.g.,



rest-rotation grazing). All these “improvements” were designed to distribute livestock utilization more uniformly across the land, gain greater efficiency of food and fiber production, and divert livestock from the especially sensitive riparian areas (Elmore and Kauffman 1994, Laycock 1995). The net result has been progressively more widespread yet intensive use of a landscape that has become at least partially tamed from the wild. These assumptions need to be reexamined in the light of biodiversity concerns. Let us continue our consideration of these relationships in the mostly highly altered sagebrush steppe areas.

If accelerated soil erosion does not ensue and the fundamental potential of the site does not change, then State III can be maintained or managed toward States II or IV. However, as herbaceous plants, litter, and microphytes in the interspaces between perennials are reduced, soil aggregate stability declines, infiltration of precipitation diminishes, overland flow increases, and soil erosion frequently increases (Blackburn et al. 1992). When a probable threshold is exceeded, the site can irreversibly change to one of lesser potential. This explains the dashed line and downward arrows below States III and IV as permanent transitions, where the syndrome of desertification is most evident.

All the previously discussed states shown above the dashed line of Fig. 3 can be dealt with via management approaches using “soft” energy. Once this threshold is exceeded, however, subsequent management requires expensive, risky, “hard” energy solutions. Unfortunately, it is often easier to get political attention after major damage has been done rather than getting budgets and personnel to plan, monitor, and tweak the healthier, more natural systems at opportune times.

Desertified Sagebrush Steppe (State V)

The desertified sites are usually initially dominated by taller, thickened brush and have largely introduced annuals in their understory. The major adventive from 1870 onward has been cheatgrass (*Bromus tectorum*) (Billings 1990, Knapp 1996). I estimate that State V comprises about 25% of the current sagebrush steppe region (Fig. 4). Removal of livestock usually only hastens further degradation from State V because livestock remove part of the herbaceous fuel load and thus reduce the chance of fire destroying the sagebrush and the spots of enriched soil it protects (Charley and West 1975). Cheatgrass fundamentally changes the fire regime (Fig. 2), and most sagebrushes, not being root sprouters, only return slowly, if ever. Livestock can be used in the spring to reduce cheatgrass (Mosley 1996); however, grazing at that time also impacts any remaining native herbs. Where there are warm season (C₄) grasses and forbs, heavy livestock grazing in the spring with deferment in summer can be used to favor the recovery of those components (R. Budd, personal communication, 1999).

Introduced Bunch Grasslands (State VI)

If insufficient amounts of native grass remain in the sagebrush steppe to allow a reasonably short return to other desired plant communities, the usual response by land management agencies has been to destroy the sagebrush and replace it mechanically (T₇) with introduced wheatgrass and ryegrass, especially crested wheatgrass (Asay 1987). This has been done because the seed of introduced perennial grasses is more readily available and less expensive and their seedlings are much more easily established than the native grasses. They also grow quickly to provide more forage with a higher nutritional plane. The introduced perennial grass stands are also much more tolerant of subsequent heavy livestock use and last for many decades (Johnson 1986). There are some long-range concerns, however (Lesica and DeLuca 1996), because the introduced perennial grasses suppress the return of natives and, thus, richer plant species assemblages. Some large treatment areas are essentially monocultures of Eurasian perennial grasses (State VI, Fig. 3). I estimate about 5% of the original sagebrush steppe has already been transformed to State VI (Fig. 4).

Wildlife biologists have noted declines in the numbers of birds (Olson 1974; Reynolds and Trost 1979, 1981), small mammals (Reynolds and Trost 1979), and large reptiles (Reynolds 1979) on such seedings of introduced grasses in the sagebrush steppe area. It should be noted, however, that such studies present a worst-case scenario because samples came from the center of large treatments. Provision for increased diversity near edges (Thomas et al. 1979) is not usually mentioned in such studies. Present-day, more sensitized planners would provide for optimum edge effect and patchiness (McEwen and DeWeese 1987, Paige and Ritter 1999).

When society made the investment in repairing severely damaged sagebrush steppe, e.g., creating perennial grass-dominated pastures of species palatable to livestock (T₇) with much greater productivity, this compensated for livestock reductions and other management restrictions on lands where States II, III, and IV (Fig. 3) predominated. Because introduced grass pastures can take much heavier utilization in the spring than the native shrub steppe, livestock can be grazed on native sagebrush steppe in fall or winter with less impact, especially on the native herbaceous perennials.

Shrub-Reinvaded Introduced Grasslands (State VII)

Introduced perennial grass plantings in the sagebrush steppe region, especially if grazed by livestock, will eventually experience shrub reinvasion (T₈ to State VII, Fig. 3), largely in response to intensity and timing of livestock grazing. I estimate (Fig. 4) that about 5% of the sagebrush steppe region is currently represented by shrub-reinvaded introduced wheatgrass/ryegrass pastures (State VII).



Shrubs reinvading State VII are not being eliminated by herbicides, as was once attempted. All herbicide use in such circumstances on public lands has been suspended by judicial decree in the Pacific Northwest. Prescribed burning of the coarser, introduced grasses is difficult and leaves patches where the shrubs prevail. Therefore, there are opportunities to enhance edge effects in large areas that were formerly homogenized. As in the untilled native areas, patchy burning could enhance wildlife habitat across landscapes by providing a mix of successional stages over a landscape, providing both cover and forage for either featured species or total species richness (Maser et al. 1984). For example, some success has been attained in creating alternate leks for sage grouse following disturbance (Eng et al. 1979). Some crested wheatgrass pastures on U.S. Forest Service lands in north-eastern California have recently been plowed and planted with native herbs in an attempt to enhance biodiversity. Aggressive annuals such as yellow starthistle were the dominant result (J. Young, USDA ARS, personal communication).

Annual Grasslands (State VIII)

Despite greatly increased attention to fire prevention and control, much of the depauperate sagebrush steppe (State V) has been burned (T_{10}) at least once during the past three decades and is now almost completely replaced by introduced annuals, mainly grasses such as cheatgrass and medusahead (State VIII, Fig. 3). The Bureau of Land Management (M. Pellant, Bureau of Land Management, personal communication) estimates that about 3 million acres of public lands in Idaho, Utah, Oregon, and Nevada are now dominated by cheatgrass and medusahead. I estimate that about 25% of the total sagebrush steppe has made these transitions (T_{10} , T_{11}).

Because of their short stature, restricted nutritional characteristics (short period of above-ground greenness), and greater susceptibility to recurring fires and drought than sagebrush steppe, such areas are undesirable from all viewpoints (Knick and Rotenberry 1997). Without nutritional supplementation, livestock can graze State VIII only during the short, early-spring growing season. Winter use is possible only in the lower-elevation areas near the Columbia River (Mosley 1996). Only the most generalist animals, such as the introduced chukars, horned larks, grasshoppers, and deer mice, seem to thrive on the annual grasslands (Maser et al. 1984). When such areas burn in early summer, soils are bared to wind and water erosion during the convectional storms of summer. The consequent needs for revegetation after fire are increasing while the budgets of federal land management agencies decline and pressure increases from environmentalists who are against proactive management.

Land dominated by annuals may provide fair watershed protection during years without fire and actually

appear to be more productive of total plant biomass than the original sagebrush-native perennial grass and forb combination (Rickard and Vaughn 1988). This is likely, however, to be only a temporary situation based on the priming effect of decomposing litter (Lesica and DeLuca 1996) and the mineralization of nutrients from the enormous below-ground necromass of the original system. The formerly strong link of net primary production with precipitation becomes decoupled (Whitford 1995). The shrub-centered islands of fertility (Charley and West 1975) are now diluted in a horizontal direction by the interactions of fire, soil erosion, and tillage. When these reserves of nutrients and soil organic matter are finally respired away, the annual grasslands are likely to become much less productive. Similar transitions happened in the Middle East several millennia ago (Zohary 1973). Many other more noxious weeds from that region could find their way here, and we could witness a downward spiral of further degradation (T_{12}).

REPAIRING THE DAMAGE

Rather than allowing the annual grasslands derived from former sagebrush steppe (State VIII, Fig. 3) to remain and the land to degrade further, some land managers are attempting to intervene. A joint program among the USDA Forest Service, Bureau of Land Management, Agricultural Research Service, and University of Idaho has been under way this past decade to reduce these threats (Pellant 1990). The most notable component of this effort is the greenstripping program, which is particularly evident in southern Idaho. The basic approach is to begin breaking up the now vast stretches of cheatgrass and other annual dominance that have developed as fires have become earlier, larger, and more frequent (Fig. 2). Land managers are attempting to break the cheatgrass-dominated areas into smaller, burnable units, especially in proximity to cities and towns. The approaches used thus far include planting strips of vegetation that stay green (and thus wetter and less burnable) longer than cheatgrass.

Although the introduced wheatgrasses, ryegrasses, and forage kochia (*Kochia prostrata*) do stay green longer and burn less readily because of coarser above-ground structure, they are not native and thus are rejected as replacements by some interest groups. Because the genetic biodiversity of the native plants is so primitively understood, the best that can be done is to gather such seed locally and plant it on comparable sites. Such seed sources are undependable, however. Thus, a root-sprouting big sagebrush is seen as a potentially better keystone species to put back in this area. A few sagebrushes may actually help sustain perennial grasses by harboring the predators on black grass bugs (*Labops* spp.) (Haws 1987). Furthermore, total plant community production can be enhanced (Harniss and Murray 1973) because sagebrushes help trap blowing snow (Sturges 1977) and



scattered sagebrushes moderate temperatures (Pierson and Wight 1991), benefit the reestablishment of native herbs, and protect them from excessive utilization (Winward 1991). Sagebrushes also harbor mycorrhizal fungi (Wicklow-Howard 1989), which helps them extract nutrients from deep in the soil and recycle them to the surface through litter production (Mack 1977, West 1991).

Whether or not we can accomplish restoration of sagebrush steppe (T_{13} , between States V and III in Fig. 3) is highly questionable. Even where funding is less limiting and topsoil is replaced on coal strip mines, early results are only partially encouraging (Hatton and West 1987). We must learn much more about how sagebrush steppe ecosystems are structured and how they function, and we must have access to vast budgets and more trained personnel before such efforts are routinely successful. It is cheaper and more feasible to foster good stewardship of land having late seral vegetation (manage while in States I, II, III, or IV of Fig. 3) rather than rely on restoration efforts after degradation has taken place (States V, VI, VII, and VIII of Fig. 3).

The future of the sagebrush steppe region is the concern of this volume. Can the damage of the past be reversed or mitigated? Is restoration or rehabilitation possible and affordable? Remember that we have lost some pieces, gained new ones, and have a new and further changing environment. New invaders, increased temperatures, atmospheric CO_2 , and UV_B pose additional problems.

While we must acknowledge that unrestricted livestock grazing, especially during droughts, was the funda-

mental cause of degradation of most sagebrush steppe, it doesn't automatically follow that reduction or even entire removal of livestock will reverse the changes for highly altered sagebrush steppe (below the dashed line in Fig. 3). Most of this land area has had threshold-exceeding changes. Soils, their nutrient pools and water handling capabilities, seed reserves, and thus their vegetation-producing potential have been fundamentally lowered. Even removing livestock during droughts will not suffice in attaining recovery. In fact, removal of livestock during wet years may increase the risk of wildfires, further damaging on-site features, as well as those at some distance, through wind erosion (dust storms). If livestock are totally removed, I predict we will have to eventually pay for them to return. The point is to constructively use them as tools within a holistically conceived recovery plan.

We must break the positive feedbacks, which allow further damage to the sagebrush steppe. The major linkage is between cheatgrass and larger, earlier, and more frequent fires (Fig. 2). I suggest further expansion of greenstripping with further use of the herbicide OUST® to reduce cheatgrass competition and allow better shrub establishment. A resprouting sagebrush would be desirable. If not that, rabbitbrushes are better than cheatgrass. Unpalatable strains of bluebunch wheatgrass (e.g., Whitmar) could be replanted to prevent overuse by livestock in the future. Let's enlist the genetic engineers to build us some perennial plants that better capture and conserve the resources that are truly irreplaceable – the soils. With the soils in place, future generations will have more options as new science and technology become available.

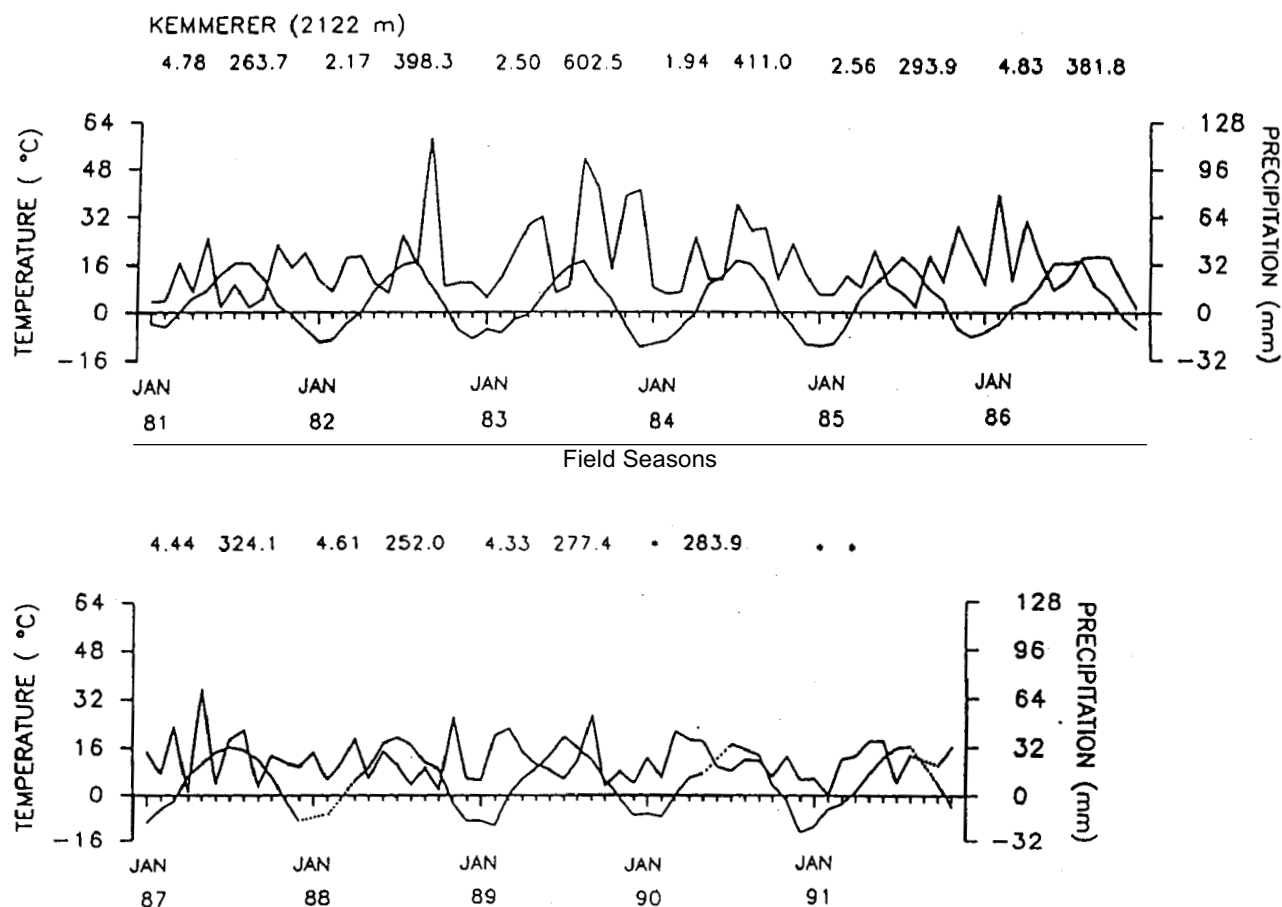


Figure 1. Patterns of mean monthly precipitation and temperature at Kemmerer, Wyoming, 1981 to 1991. Mean annual temperature (°C) and total annual precipitation (mm) are the numbers entered above the trend lines for each year.

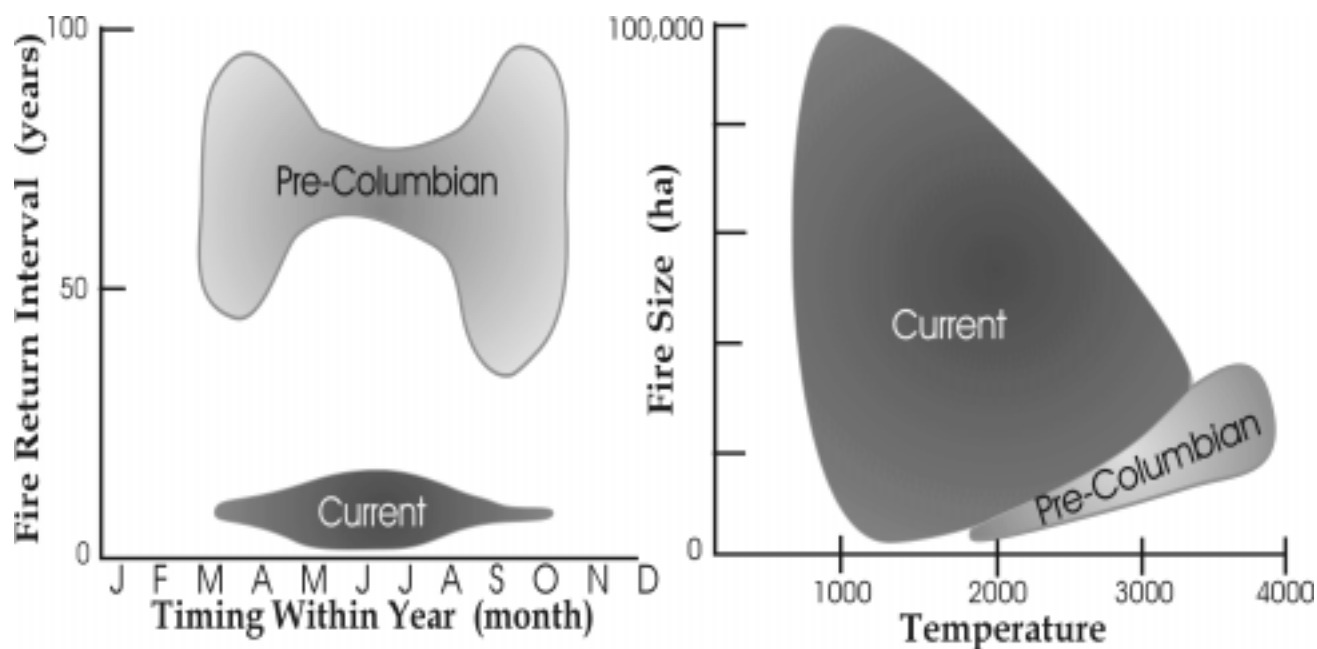


Figure 2. Estimated differences in the fire regime of sagebrush steppe in Pre-Columbian and current times.

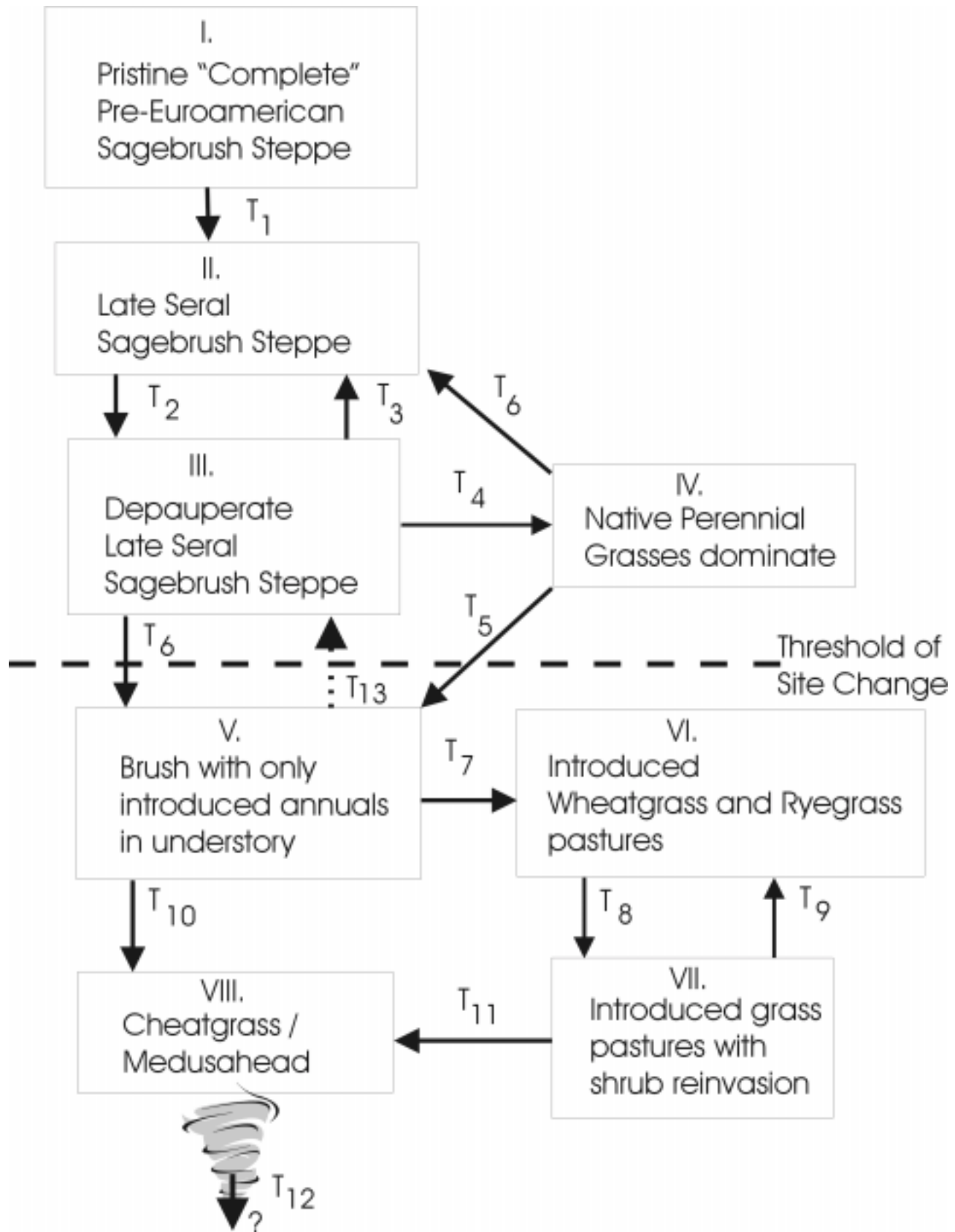


Figure 3. State and transition model of successional change in sagebrush steppe (from West 1999, permission to reprint from CRC Press).

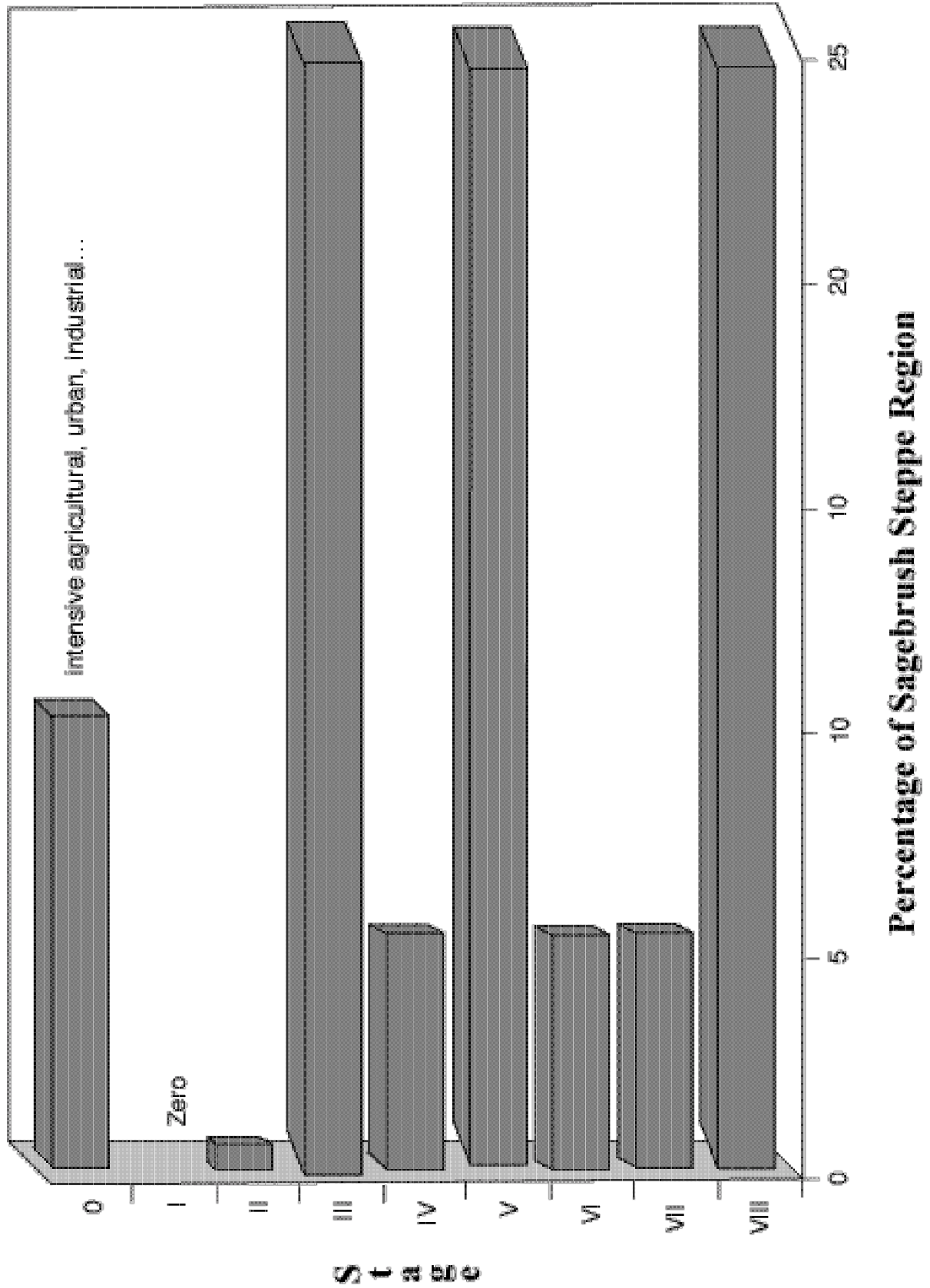


Figure 4. Percentages of the Pre-Columbian sagebrush steppe that are estimated to be occupied by the various states of Figure 3.



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SAGEBRUSH STEPPE WILDLIFE: HISTORICAL AND CURRENT PERSPECTIVES

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INTRODUCTION

The sagebrush (*Artemisia* spp.) steppe ecosystem harbors about 250 species of terrestrial vertebrates, the majority being birds and mammals, with approximately 100 and 70 species, respectively (Braun et al. 1976). Many species that were formerly common and abundant now have restricted ranges separated by a vast landscape of agricultural developments and nonnative grasslands. While there are currently no federally listed wildlife species under the Endangered Species Act that would be considered sagebrush steppe obligates, some significant, formerly wide-ranging species such as the Columbian sharp-tailed grouse (*Tympananuchus phasianellus columbianus*) and sage grouse (*Centrocercus urophasianus*) (Washington State population only) have been petitioned for listing as threatened or endangered. A significant number of sagebrush steppe wildlife species are also identified as species of concern by federal land management and state wildlife agencies due to significant declines in distribution and abundance (Rich 1999). Nearly all declines of native sagebrush steppe vertebrates are closely associated with habitat loss or degradation.

Twenty-nine tall sagebrush communities and 14 short sagebrush communities have been described for the sagebrush steppe (Blaisdell et al. 1982). Precipitation, elevation, and soil conditions are major factors that influence the distribution of these communities. The structure and composition of plant species vary greatly within and among these communities (Daubenmire 1970, Franklin and Dyness 1973, Hironaka et al. 1983, Anderson 1986). This heterogeneity creates a variety of ecological niches for wildlife (Dealy et al. 1981, Paige and Ritter 1999).

Wildlife habitat alterations (loss, degradation, and fragmentation) within the sagebrush steppe ecosystem have been and continue to be common and widespread.

Major historical losses of sagebrush steppe occurred as a result of conversion to agricultural cropland, especially in eastern Washington and southern Idaho (Wisdom et al. In Press). During the middle decades of this century, millions of hectares were treated to convert sagebrush areas to nonnative grasslands for livestock forage production. More recently, extensive wildfires have converted millions of hectares to nonnative annual grasslands, especially in eastern Oregon, southern Idaho, and northern Utah and Nevada (Pellant and Hall 1994). As early as 1978, the combined effects of these historic alterations resulted in a 55% loss of the sagebrush steppe in Idaho (Sharp and Sanders 1978). Today, scientists estimate that sagebrush steppe habitat has been reduced by 1/3 in the interior Columbia River Basin ecoregion (Wisdom et al. In Press).

The patchwork of sagebrush areas remaining today is a landscape of habitat islands for sagebrush obligate species. Many remaining sagebrush communities are small and widely separated from each other. This habitat fragmentation has important implications to wildlife, especially those that are migratory and dependent on large sagebrush areas. For example, loss of low elevation sagebrush areas that provide crucial winter habitat for species such as sage grouse or mule deer (*Odocoileus hemionus*) can have a disproportionate effect on the population health of these species over a very large area (Swenson et al. 1987, Thomas and Irby 1990, Dobkin 1995).

Nearly all the remaining sagebrush steppe is ecologically degraded (West, this volume). Unregulated livestock grazing in the early 1900s resulted in a reduced herbaceous understory, subsequent decrease in the natural fire frequency, and a commensurate increase in sagebrush cover (Blaisdell et al. 1982, Young 1994). In some mesic sagebrush areas, this has also provided conditions suitable for expansion of conifers (*Juniperus* spp., *Pseudotsuga menziesii* and *Pinus* spp.) into sagebrush areas (West and Van Pelt 1987). In many areas, the reduction in native ground covers also created conditions suitable for non-native annual grasses (Blaisdell et al. 1982, Young 1994).

These habitat alterations have caused considerable alarm among conservation biologists. Ungrazed shrub steppe has been recognized as a "critically endangered

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ecosystem” due to a loss of more than 98% from historical times (Noss et al. 1995). Similarly, the World Wildlife Fund ranked the Columbia Plateau and Wyoming Basin ecoregions, the 2 ecoregions encompassing most of the sagebrush steppe, as endangered and vulnerable, respectively (Ricketts et al. 1999). They considered the Columbia Plateau ecoregion as an area of very high biological importance. Habitat loss and significant threats of additional losses were the primary factors in their assessment. Although they did not rank the Wyoming Basin at the same level of biological importance or threat, the vulnerable rating was based on impending increase of energy and mineral development.

In this paper we briefly discuss the pristine habitat-wildlife conditions (defined as that which existed prior to or just after European settlement). We then summarize species-habitat relationships associated with the various ecological states of sagebrush steppe condition as defined by West (this volume). Fragmentation and other factors affecting wildlife populations and habitat are discussed. We recommend actions that should be initiated immediately to reverse the current trend of habitat loss and degradation.

PRISTINE VEGETATION, WILDLIFE ABUNDANCE AND DISTRIBUTION

Most range scientists agree that sagebrush steppe communities generally had a vigorous herbaceous layer of perennial grasses and forbs intermixed with a moderate sagebrush cover at the time of pre-European settlement (Franklin and Dyrness 1973, Harniss and Murray 1973, Vale 1975). In eastern Washington, Daubenmire (1970) found that relic big sagebrush (*Artemesia tridentata* ssp. *tridentata*)/bluebunch wheatgrass (*Pseudoroegneria spicata*) and big sagebrush/Idaho fescue (*Festuca idahoensis*) stands had an average canopy coverage of bluebunch wheatgrass and/or Idaho fescue of 45% and 58%, respectively; sagebrush canopy coverage averaged 14% (9 to 19%). After 25 years of grazing exclusion in a more xeric Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*) site in eastern Idaho, Anderson and Holte (1981) reported the average basal coverage of perennial grasses at 6%, with total shrub canopy cover at 27%.

With a basic understanding of the pristine vegetative conditions and a knowledge of species-habitat relationships, some inferences can be made regarding historical wildlife habitat (Wisdom et al. In Press). Historical accounts from early explorers and pioneers are useful in reconstructing the original distribution of wildlife, but using them as descriptors of “natural” abundance should be avoided, especially for large mammals. Prior to European exploration and settlement, large mammal populations may have existed at levels below habitat potential due to the settlement distribution and influence of Native Americans (Martin and Szuter 1999). Trappers and early explorers in Nevada often noted a lack of large

mammals, but they also frequently noted a high degree of shyness in game (R. McQuivey, Nevada Department of Wildlife, personal communication). This shyness is a behavioral attribute typical of species experiencing a high degree of persecution.

Based on vegetation and species-habitat relationships, large mammals such as elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis californiana*) should have been relatively common in pristine sagebrush steppe (Martin and Szuter 1999). Pronghorn are a diurnal species dependent on eyesight and speed to escape predators. Under pristine conditions, extensive areas with a low coverage of shrubs would have afforded good visibility for predator escape as well as adequate biomass to meet this species’ food requirements (Yoakum 1980). Bighorn sheep are also dependent on keen eyesight to detect predators but use agility rather than speed for escape (Buechner 1960). Open sagebrush stands with good herbaceous understories near cliffs and other broken terrain offered very good habitat conditions for this species. Indeed, many of the relic sagebrush areas remaining today are associated with inaccessible canyonlands and other rugged habitats that are bighorn sheep source habitats.

In the Great Basin region, black-tailed jackrabbits (*Lepus californicus*) were the most abundant large herbivore (McAdoo and Young 1980, Wagner 1981). However, although jackrabbits were abundant during population peaks under pristine habitat conditions, they were never as abundant as they later came to be with the advent of farming and the increase in sagebrush resulting from livestock grazing (McAdoo and Young 1980).

Historically, sage grouse were widely distributed and abundant in many areas (Schroeder et al. 1999). The diversity of sagebrush cover and density of herbaceous ground cover must have provided ideal conditions. Many anecdotal references associated with the fall migrations of birds refer to hundreds and even thousands of birds (Patterson 1952). In 1886, naturalist G.B. Grinnell reported that literally thousands of birds passed by him one fall day in western Wyoming, reminding him of the flights of passenger pigeons (full quotation in Patterson 1952).

The mesic portions of the sagebrush steppe historically supported large numbers of Columbian sharp-tailed grouse (Connelly et al. 1998). Numerous reports from explorers and pioneers noted the high abundance of sharptails, even more so than sage grouse in some areas. Sharptails were frequently reported as the most abundant game bird in eastern Washington (Yocom 1952), eastern Idaho (Rust 1917), and northern Utah (Lee 1936).

WILDLIFE AND SAGEBRUSH STEPPE ECOLOGICAL STATES

Range ecologists recently have identified 8 ecological states for sagebrush steppe plant communities (West, this volume). These ecological states range from pristine



(State I) to annual grasslands (State VIII). We provide a brief overview of the native wildlife community within each of these ecological states, frequently comparing habitat conditions to pristine conditions (State I) as a frame of reference. Information concerning wildlife responses to these various states was often limited to birds and mammals; data on reptiles and amphibians are scarce.

Pristine (State I) and Relic (State II) Sagebrush Steppe

Pristine conditions likely no longer exist, and relic areas are thought to constitute less than 1% of the remaining sagebrush steppe habitat (West, this volume). Relic sites are areas characterized by open sagebrush stands with an abundant perennial herbaceous cover (West, this volume), similar to pristine conditions. The heterogeneous shrub-grassland habitats (Daubenmire 1970) provide generally good biological diversity (Dobler 1994) and diverse niches for shrub- and ground-nesting birds (McAdoo et al. 1986). Although these areas make up a small proportion of the landscape, they are usually associated with other sagebrush-dominated communities and are often important source habitats for sagebrush steppe species that prefer more open sagebrush cover (e.g., bighorn sheep, pronghorn, and sharp-tailed grouse).

Sagebrush with a Depleted Herbaceous Layer (State III)

Sagebrush areas with depleted understories occupy approximately 25% of the sagebrush steppe landscape (West, this volume). Wildlife preferring dense shrub cover (>20%) with little herbaceous understory for nesting or foraging would be favored in this ecological state. Habitat in this state may have a similar wildlife species richness as relic areas; but abundance, especially for ground-nesting birds, would likely be reduced (McAdoo et al. 1986).

Numerous studies on sage grouse have demonstrated the critical importance of sagebrush for both food and cover (Connelly and Braun 1997, Schroeder et al. 1999). Sagebrush cover is essential for nesting and wintering habitats, characterized by average canopies between 10% and 30%. However, it is becoming increasingly clear that a vegetatively diverse sagebrush community with native perennial understory may provide the best habitat for nesting sage grouse (Apa 1998, Schroeder et al. 1999).

Most remaining sage grouse habitat is in this ecological state with varying degrees of understory depletion. Poor nesting habitat conditions have been a documented wildlife management concern for many years (Patterson 1952, Autenrieth 1981). Nest predation rates have been reported as significantly higher in sagebrush stands with a depleted perennial herbaceous layer (Connelly et al. 1991, Gregg et al. 1994, Delong et al. 1995, Sveum et al. 1998).

Sage thrashers (*Oreoscoptes montanus*) showed a positive relationship to an understory of bluebunch wheatgrass (Dobler 1994). Other ground-nesting birds such as

vesper sparrow (*Pooecetes gramineus*) and western meadowlark (*Sturnella neglecta*) occur at much lower densities in sagebrush stands with a depleted native herbaceous understory (Wiens and Rotenberry 1981, Petersen and Best 1987).

The percent sagebrush cover has important influences on habitat use by many bird species. Of 17 birds studied in eastern Washington, 7 species had a positive relationship to sagebrush cover, 2 were inversely related, and 8 were not related (Dobler 1994). Species benefiting from sagebrush cover included Brewer's sparrow (*Spizella breweri*), sage sparrow (*Amphispiza belli*), sage thrasher, loggerhead shrike (*Lanius ludovicianus*), brown-headed cowbird (*Molothrus ater*), and mourning dove (*Zenaidura macroura*). Species with a negative relationship were savannah sparrow (*Passerculus sandwichensis*) and long-billed curlew (*Numenius americanus*).

Black-tailed jackrabbits, strongly dependent on shrubs, have expanded their range, whereas in contrast, the distribution of white-tailed jackrabbits (*Lepus townsendii*), a species more dependent on grass, has diminished (McAdoo and Young 1980). However, on a finer scale, black-tailed jackrabbit populations have been significantly reduced where wildfire has eliminated sagebrush stands in the Snake River Plain (USDI 1996, Knick and Dyer 1997).

Native Perennial Herb-Dominated Stands (State IV)

This state is considered transitional and occurs after burns or other shrub-removal treatments. Less than 5% of the sagebrush steppe is in this state (West, this volume). Grassland bird species such as vesper sparrow, western meadowlark (Wiens and Rotenberry 1981, Castrale 1982), and sharp-tailed grouse (McDonald 1998) are favored in this state, although its value to wildlife depends on local conditions often related to the intensity and timing of livestock use (Saab et al. 1995).

No differences were reported in total density or biomass of songbirds following a sagebrush fire, although species composition changed dramatically (Wiens and Rotenberry 1981). Horned lark (*Eremophila alpestris*) replaced sage sparrow as the most abundant breeding bird. Nongame bird species richness and abundance increased 4 years after a mosaic-pattern prescribed burn in eastern Idaho (Peterson and Best 1987). One ground nester increased in abundance, and 2 species colonized the burn areas. However, a similar prescribed burn in the same region has resulted in the continued depression of a nesting sagegrouse population 9 years after the burn (Connelly et al. 1994).

Sagebrush with an Annual Herbaceous Layer (State V)

Approximately 25% of the sagebrush steppe landscape is now thought to be occupied by sagebrush with an understory dominated by nonnative annual grasses (West, this volume). Sagebrush communities in this state are extremely vulnerable to loss and permanent



transition to State VIII as a result of wildfires (Pellant 1990; Shaw et al. 1999; West, this volume).

Sagebrush canopy cover and structure may be similar to State III areas, but herbaceous conditions are significantly different. Understory vegetation of nonnatives provides marginal nesting cover for ground-nesting birds such as sage grouse, sharp-tailed grouse, vesper sparrow, and western meadowlark (McAdoo et al. 1986, Saab and Marks 1992, Dobler 1994, Saab and Rich 1997). Nesting conditions for these species are particularly adverse during drought periods when annual grasses would provide only limited concealment. Four of 7 bird species studied in shrub steppe habitats of eastern Washington showed an inverse relationship to annual grass cover, and no species showed a positive relationship (Dobler 1994). The most common sagebrush obligates found in these sites are shrub nesters, including Brewer's sparrow, sage thrasher, and sage sparrow (Dobler 1994, Knick and Rotenberry 1995).

Introduced Perennial Grass (State VI)

Approximately 5% of the sagebrush steppe landscape is now in this state due to fire rehabilitation efforts and land treatments for forage production. Until recently, rehabilitation efforts of degraded rangelands largely involved the use of nonnative perennial grasses, usually as a single species. The most widely used grass has been crested wheatgrass (*Agropyron cristatum*), although intermediate wheatgrass (*A. intermedium*) has been used extensively in mesic sagebrush steppe sites (generally >30.5 cm [12 inches] annual precipitation). Seedlings within the past 10 to 15 years usually involved multiple herbaceous species. Although some seedlings included native grasses and shrubs, the use of native shrubs, grasses, and forbs is still quite limited.

Few if any wildlife studies have been done on multiple-species seedlings. Studies have shown that single-species nonnative grasslands provide poor habitat for native sagebrush steppe birds. Nesting western meadowlarks and vesper sparrows were more abundant in native perennial grasses than in crested wheatgrass seedlings (Wiens and Rotenberry 1981). Total bird species density, richness, and diversity in crested wheatgrass stands in southeastern Idaho were lower than in nearby sagebrush habitats (Reynolds and Trost 1980). Horned larks (*Eremophila alpestris*), western meadowlarks, and vesper sparrows were found nesting in ungrazed crested wheatgrass seedlings, but nothing is known about their reproductive success.

Seedlings may function as habitat sinks, where mortality exceeds reproduction (cf. Saab and Rich 1997). In eastern Washington, Columbian sharp-tailed grouse selected crested wheatgrass for nesting. Their nest success, however, was only 18% (n=11), whereas nest success in native grass and shrub habitats was 100% (n=6) (McDonald 1998). McDonald (1998) considered

crested wheatgrass seedlings to be habitat sinks for sharptails and recommended their replacement with native bunchgrass and forb species.

Other nonnative grasses may not provide good habitat for sharptails. Columbian sharp-tailed grouse in western Idaho avoided use of an intermediate wheatgrass seedling within their home range (Marks and Marks 1987, Saab and Marks 1992). Additionally, native perennials such as bluebunch wheatgrass and arrowleaf balsamroot (*Balsamorhiza sagittata*) were highly selected cover species during a drought year (Saab and Marks 1992).

Ungrazed nonnative grasslands seeded through the federal Conservation Reserve Program have provided nesting and brood-rearing habitat for Columbian sharp-tailed grouse in southeastern Idaho (Idaho Department of Fish and Game, unpublished data). However, seedlings containing dryland alfalfa (*Medicago sativa*) or with an abundance of annual forbs had greater use by sharptails than seedlings that were predominantly grasses (Ulliman 1995).

Numbers of small mammals and reptiles also have been reduced in nonnative seedlings. In southeast Idaho, lower rodent and reptile densities were found in crested wheatgrass seedlings compared to sagebrush stands (Reynolds and Trost 1980).

Sagebrush with an Introduced Perennial Grass Understory (State VII)

Approximately 5% of the sagebrush steppe landscape is thought to be older nonnative grass seedlings with some sagebrush (West, this volume). Little data are available on responses of wildlife to sagebrush re-establishment into these areas. In a central Nevada study, species richness was greater where sagebrush had established into crested wheatgrass seedlings than in either monoculture seedlings or high-coverage sagebrush habitats (McAdoo et al. 1986). Comparable levels of abundance may not occur, however, unless microhabitat structure is similar to that of native plant species (see discussion in previous section, State VI). The ecologically simpler habitat is likely to have a lower wildlife diversity than sagebrush with an understory of native grass and forb species.

Annual Grasslands (Type VIII)

Annual grasslands now occupy more than 25% of the sagebrush steppe landscape, and this statistic is growing (West, this volume). Most sagebrush steppe species have not benefited from the loss of shrubs and the dominance of annuals (Dobler 1994). Shrub obligate species such as Brewer's sparrows and sage grouse largely disappear from previously occupied areas. Direct impacts to shrub-nesting species occur with the loss of nesting and foraging substrates. Some species of non-game birds that are not dependent on shrubs for nesting either decline or are eliminated by the loss of shrub cover.



In south-central Idaho, songbird community composition and density were dramatically altered in cheatgrass (*Bromus tectorum*) compared to native sagebrush cover (T. Rich, unpublished data in Shaw et al. 1999). From 1981 to 1985, species richness averaged 8.4 to 10.2 in sagebrush stands while nearby cheatgrass stands averaged 1.5. Breeding densities were also strikingly reduced in cheatgrass stands. Densities averaged 0.6 to 1.1 birds/ha in cheatgrass compared to 3.9 to 8.1 birds/ha in sagebrush. Small mammal populations in a cheatgrass-dominated rangeland in Washington were only 1/3 as abundant as those on adjacent sagebrush/bitterbrush (*Purshia tridentata*)-dominated sites (Gano and Rickard 1982).

Studies in the Snake River Birds of Prey National Conservation Area (NCA) in southwest Idaho suggest that golden eagles (*Aquila chrysaetos*) and prairie falcons (*Falco mexicanus*) in the NCA have been adversely affected by changes in prey species abundance as a result of annual grassland expansion and corresponding loss of sagebrush cover (USDI 1996, Marzluff et al. 1997, Kochert et al. 1999, Steenhof et al. 1999). Black-tailed jackrabbit population declines were closely correlated with a loss of sagebrush cover, and current distribution was related to remaining habitat (USDI 1996, Knick and Dyer 1997). Densities of Paiute ground squirrels (*Spermophilus mollis*) (formerly Townsend's ground squirrels [*Spermophilus townsendii*]) in the same area could be high even with the loss of sagebrush cover and dominance of annual grasses. Researchers, however, found that squirrel populations fluctuated more dramatically in areas that had been converted to annuals. Populations were more stable in sagebrush communities with a residual component of native herbaceous perennials in the understory (USDI 1996).

At least 2 bird species have apparently benefited from the expansion of annual grasslands. Long-term breeding-bird census data indicate that long-billed curlews and western burrowing owls (*Speotyto cunicularia*) have increased in recent decades (Saab and Rich 1997, Wisdom et al. In Press). Cheatgrass and medusahead (*Taeniatherum caput-medusae*) are suitable for these species because they favor open habitats with short vegetation. However, these population gains may be short-lived. The rapid replacement of cheatgrass- and medusa-infested ranges with taller exotic annual forbs may render these sites unsuitable to these species (Shaw et al. 1999).

Annual Forb-Dominated Stands (Proposed State IX)

Large areas are now becoming dominated by exotic annual forbs such as yellow starthistle (*Centaurea solstitialis*), knapweeds (*Centaurea* spp.), rush skeletonweed (*Chondrilla juncea*), and other exotics. Perhaps we are beginning to see yet another sagebrush steppe state that represents a greater magnitude of degradation for this ecosystem and its associated wildlife.

The consequences of transformations to this state of ecological degradation are largely unstudied, but the implications are particularly onerous to wildlife.

INFLUENCES OF HABITAT FRAGMENTATION

Sagebrush patch sizes, surrounding landscapes, and connectivity of suitable habitats are critical to the long-term persistence of many sagebrush steppe species. Habitat fragmentation and patch sizes may influence wildlife use and productivity as much as microhabitat conditions (Knick and Rotenberry 1995). For example, sagebrush patch sizes influenced black-tailed jackrabbit distribution in the Snake River Birds of Prey Area (Knick and Dyer 1997), which in turn affected the distribution, habitat use, and productivity of golden eagles (Marzluff et al. 1997, Kochert et al. 1999).

Some sagebrush steppe species require thousands of hectares to support viable populations. These area-sensitive species include both large and medium-sized mammals and birds such as sage grouse and sharp-tailed grouse. This is not to imply that their habitat must be either all in relic condition or all in sagebrush habitats. Indeed, some species like mule deer and black-tailed jackrabbits may flourish in moderately degraded habitat, and others such as pronghorn may sustain low-density populations in annual grasslands.

Within the interior Columbia Basin, major loss and fragmentation of sage grouse habitat has occurred since settlement (Fig. 1) (Wisdom et al. In Press). Similarly, landscape analysis of historic and current Columbian sharptail habitat in eastern Washington revealed that their habitat has declined 83%, while their distribution has decreased 89% (McDonald and Reese 1998). Additionally, the number of habitat patches nearly doubled and mean habitat patch size declined 36%, from 4,474 ha (11,051 acres) to 2,857 ha (7,057 acres) (McDonald and Reese 1998). As a result of fragmentation, the mean distance between populations is currently 61 km (38 miles), triple the dispersal distance of female sharptails.

Sage grouse and sharp-tailed grouse need thousands of hectares of adequately connected habitat to support self-sustaining populations (Paige and Ritter 1999). An estimated 3,000 ha (7,400 acres) are needed to support a population of sharptails, with at least 33% of the area undisturbed habitat imbedded within other habitats that provide some value to the species (Connelly et al. 1998). Sage grouse, with their narrower habitat requirements and virtual dependence on sagebrush, are likely to require larger and more continuous sagebrush habitats than sharptails.

Within the Snake River Birds of Prey National Conservation Area, fragmentation of shrub steppe significantly influenced the presence of shrub-obligate species (Knick and Rotenberry 1995). They found that sage sparrows, Brewer's sparrows, and sage thrashers were all sensitive to the amount of shrub cover and the

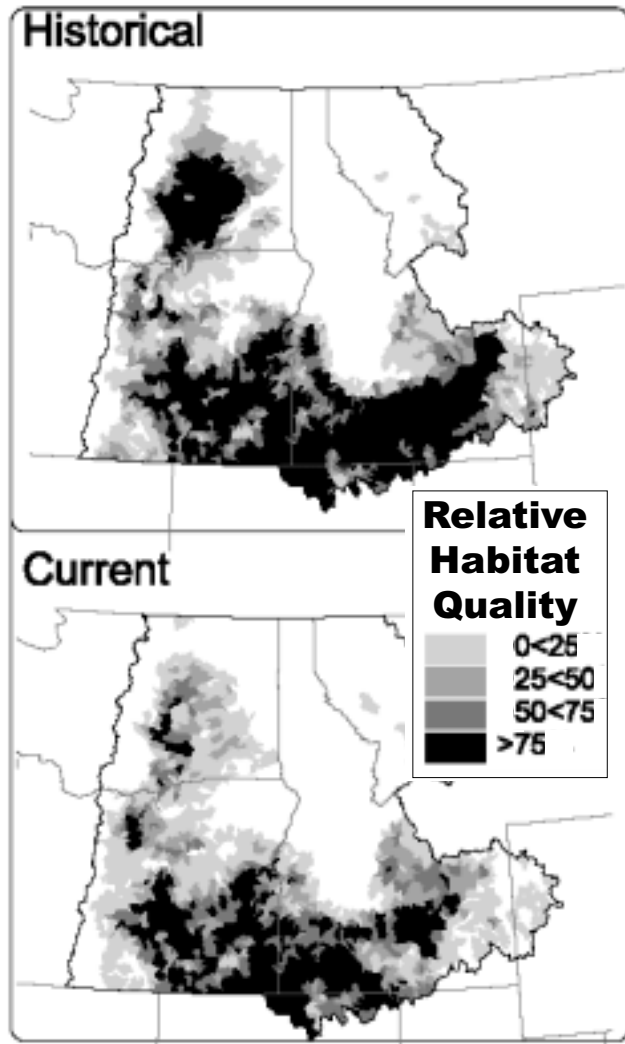


Figure 1. Historical and current sage grouse habitat, Interior Columbia River Basin (Wisdom et al. In Press).

shrub patch size. In a Washington study, sage sparrows did not occur on shrub patches less than 130 ha (320 ac) (Vander Haegan, personal communication, in Paige and Ritter 1999). To support a population, a much larger area of suitable habitat would be needed.

CONCLUSIONS

Studies of wildlife in sagebrush communities have shown consistent patterns. Ecologically intact sagebrush communities have a higher diversity of species than degraded sites (Petersen and Best 1987, Dobler 1994). Moreover, most species that are currently rare or have undergone significant declines are closely associated with sagebrush communities that are still ecologically intact (i.e., retain characteristics of unaltered sagebrush communities).

We have at least rudimentary knowledge of species/habitat relationships for many sagebrush-associated wildlife species and the range of natural variation in sagebrush

vegetative communities. We know sagebrush communities are very vulnerable to degradation and are difficult, if not impossible, to restore once certain thresholds are crossed (West, this volume). Lastly, we know that altered areas are vulnerable to further degradation, providing even less habitat for sagebrush steppe wildlife.

MANAGEMENT IMPLICATIONS

Our goal is to maintain native species biodiversity, referring to both the number of species as well as an intrinsic level of abundance that provides for long-term population persistence in the presence of expected environmental perturbations (e.g., flood, fire, and drought). Providing for the needs of area-sensitive species dependent on intact sagebrush steppe communities should provide for the needs of many other sagebrush steppe-associated species. To accomplish this, we must approach management from a landscape perspective, even though specific management actions are nearly always implemented at the local level. Local decisions should consider the landscape context when implementing management.

Assuming there will continue to be limited financial resources to accomplish wildlife diversity goals, the following recommendations are listed in priority order:

1. Identify and maintain the ecological integrity of remaining intact sagebrush steppe communities. The investment in time and resources is minimal to accomplish this while these areas are still intact.

2. Identify areas that are depleted (States III, IV, and VI) but can be restored using "soft" energy inputs (see West, this volume). Implement management actions to protect and recover these sites. Use adaptive management to monitor progress and make appropriate changes in management strategies.

3. Identify areas that are severely degraded (States V - VIII) but are key to reconnecting fragmented habitats. Restore these areas using native plants (shrubs, grasses, and forbs) as available. If nonnatives are selected, use ecotypes that closely mimic growth forms of native species. Manage land uses to maintain restored habitats and protect financial investment.

In addition, achieving additional understanding and support for sagebrush steppe conservation and accelerating applied native plant research efforts to more effectively restore depleted habitats are essential to a successful program to maintain a viable sagebrush steppe ecosystem.

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HISTORICAL SAGEBRUSH ECOSYSTEMS: HUMAN INFLUENCES

James A. Young

INTRODUCTION

The conversion of millions of hectares of sagebrush (*Artemisia*)/bunchgrass rangelands to dominance by the accidentally introduced, self-invasive annual cheatgrass (*Bromus tectorum*) is a well-documented fact. The purpose of this paper is to provide a historical perspective on how the scientific community first perceived this conversion.

SOCIAL, ECOLOGICAL, ECONOMIC SETTING

The initial establishment and rapid spread of cheatgrass in the Intermountain Region largely occurred during the 1900s, with increasing dominance during the second half of the century. Until 1934, the portions of the sagebrush/bunchgrass rangelands that were not in private ownership or within a National Forest were publicly owned land open to homesteading, with no grazing management. After passage of the 1934 Taylor Grazing Act, these lands were administered by the U.S. Department of the Interior (USDI) Grazing Service and later by the USDI Bureau of Land Management. The public lands outside of the National Forests were generally the lower-elevation areas with less potential for plant growth. These lands included homesteaded areas where cropping had failed and the land was subsequently abandoned.

For the first 3 1/2 decades of this century, these vacant public lands were grazed in common by domestic cattle, horses, and sheep. Huge numbers of draft horses were turned loose on the open range during the off season for agricultural production. This was especially true near newly irrigated agricultural developments such as on Idaho's Snake River Plain. It is very difficult now to visualize and ascertain the biological impact of range sheep in the sagebrush/bunchgrass ecosystem during the first half of the 20th century. The sheep industry grew after the cattle and horse husbandry industries were already established (Young and Sparks 1985). The enterprises that owned no base property and were known as "tramp sheep" contributed to the destruction of range resources. This huge industry was superimposed upon already overstocked rangelands. Ranchers herded their cattle on sagebrush ranges to make sure that no forage went ungrazed, because if they did not utilize the resource, their neighbor – or worse yet, a "tramp sheep" outfit – would get the forage (Emmerich et al. 1992).

If you continue to excessively graze sagebrush/bunchgrass ranges season-long, 2 things will happen. First, the perennial grasses will disappear, and second, the density of big sagebrush will increase. The second is a forgotten factor in modern big sagebrush management. With virtually no herbaceous understory to help carry wildfires, the overly dense big sagebrush stands perpetuated themselves while limiting the establishment of native herbaceous perennials.

INTRODUCTION OF EXOTIC INVASIVE WEEDS

Starting with Russian thistle (*Salsola targus*), tumble-mustard (*Sisymbrium altissimum*), cheatgrass, medusa-head (*Taeniatherum caput-medusae*), and barbwire Russian thistle (*Salsola paulsenii*), the exotic self-invasive species have come in waves. They form a seral continuum that has truncated succession and led to long-term dominance by cheatgrass. The factor that invokes this dominance is stand renewal by repeated wildfires.

The truncation of succession and the relation of cheatgrass dominance to rapidly recurring wildfires was first reported by Pickford (1932). His classic paper on the spring-fall ranges of Utah dramatically reported what eventually would happen to much of the sagebrush/bunchgrass ranges of the Intermountain Region.

GRAZING MANAGEMENT WITH CHEATGRASS

Stewart and Young (1939) reported that the short "green-feed" period, great variability among years in herbage production, and potentially injurious awns made cheatgrass a hazardous species on which to base livestock production. Aldo Leopold (1941) followed with a paper stressing that the increased chance of ignition and rate of spread of wildfires fueled by cheatgrass would prove very harmful to wildlife populations. Before the Grazing Service was established, utilization of forage on the sagebrush ranges was generally so intense that cheatgrass was apparently biologically suppressed. Fleming et al. (1942) published a landmark bulletin on the value of grazing *Bromus tectorum* (they called it bronco grass). They readily admitted it was an inferior forage to the disappearing native bunchgrasses, but reality said it was the forage that supported a significant portion of the range livestock industry.

The final landmark scientific paper on cheatgrass was published by Robertson and Pearse (1945). Their premise was that cheatgrass, by out-competing the

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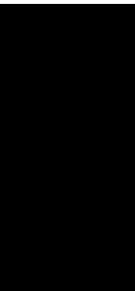


seedlings of artificially planted perennial grasses for soil moisture, was virtually closing communities to the recruitment of new perennials. Eventually it became apparent that their findings extended to virtually all perennial seedlings, not just introduced forage grasses.

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Current Issues in Sagebrush Steppe Ecosystems





CURRENT ISSUES IN THE SAGEBRUSH STEPPE ECOSYSTEM: GRAZING, FIRE, AND OTHER DISTURBANCES

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Disturbances under consideration are those that result, either directly or indirectly, from human activities in the sagebrush steppe ecosystem. Grazing by livestock as well as fire use and removal are of primary concern, although other direct activities such as recreation will be touched upon.

By definition, disturbance means a significant change has occurred in the resource base, the plant community has been moved away from a stable state, and a compositional change has occurred in both plant species and life histories. Key functional elements of any disturbance are its timing (seasonality), intensity (resource loss), abiotic resources available (water and nutrients), biotic resources available (species and their attributes), frequency (recovery interval between disturbances), and regime (connectivity to other disturbances in time and space) (Sousa 1984).

Issues surrounding grazing and fire tend to arise out of the ecological uncertainty as to whether they will produce a feedback that enforces the stability of the present community or whether they will promote transitions to a more desired community or a less desired one. Given the present state of the sagebrush steppe ecosystem, key questions center on how to influence sagebrush communities through the presence or absence of grazing and fire. The effects on vegetation and soils from overgrazing, high-frequency fires, and other factors such as uncontrolled recreational vehicle use may be rather obvious (Blaisdell et al. 1982, Bunting et al. 1987, Vavra et al. 1994). Less obvious, however, are the effects on other biota. Judicious grazing practices and prescribed fire carry with them varying degrees of uncertainty as to short-term and long-term outcomes. This degree of uncertainty can be expected, since the key functional elements of disturbance vary greatly through time. Further, in the presence of a highly variable climate, they function as a disturbance regime rather than as independent events.

In the sagebrush steppe communities of the Intermountain West, original plant communities were composed of a few dominant species, i.e., sagebrush and 1 or 2 perennial grasses, and numerous other species that were both spatially and temporally dynamic. Those few dominant species were highly competitive for limited resources and tended to produce a relatively stable sagebrush steppe ecosystem in the face of a variable disturbance regime. Their relative abundance locally and regionally was mediated largely by fire, herbivory, and climate. The abundance of the dynamic group, comprising the vast majority of sagebrush steppe species, including many forbs, was mediated by disturbances that freed up resources for establishment. Most of these species relied on seed production and dispersal as a means of maintaining their presence in the system and establishment on disturbed sites.

Current human activities, i.e., grazing, fire, and recreation, in the sagebrush steppe are not perpetuating the original plant community composition. West (1999) estimated that less than 1% of the sagebrush steppe remains in its original condition. Rather, we have a system in which disturbances cause several very different changes in species composition to occur. First, disturbance may enhance the competitive ability of one of the dominant species, i.e., sagebrush, and reduce the competitive ability of the other dominant species, i.e., perennial grass. Second, disturbance may enhance the competitive ability of one dominant, i.e., sagebrush, and eliminate the other dominant, i.e., perennial grass. Third, disturbance may cause the loss of the original dominants. In all 3 cases, one or all of the original dominants are required to function in the ecosystem similarly to the dynamic disturbance-adapted species such as cheatgrass, which they are not well adapted to do.

West (1999) used the state-and-transition model to describe current conditions in the sagebrush steppe. He recognizes 8 states that range from pristine to highly disturbed. Four of these, which we would place in the moderate to highly disturbed state, make up the vast majority of the sagebrush steppe. These 4 states, using West's model (included in this proceeding), are "*II: Late Seral Sagebrush Steppe*," "*III: Depauperate Late Seral Sagebrush Steppe*," "*V: Brush with only introduced*

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annuals in understory,” and “*VII: Cheatgrass/Medusa-head.*” States III and V together constitute over 50% of the sagebrush ecosystem. States II and VII make up most of the rest of the sagebrush steppe ecosystem.

At the heart of management are the issues of prescribed grazing and fire and their effects on transitions toward desired communities and, conversely, their effects on transitions to less desirable states. Key questions that need to be asked for each and every vegetation state are:

- What site resources are available?
- What transitions and steady states are possible?
- How do grazing and fire direct plant succession?

Those questions should form the basis of management decisions before they are implemented.

Those plant communities falling into the state *Late Seral Sagebrush Steppe* should be considered for maintenance of the vegetation community. Even here, perceptions of biodiversity and health may push managers to consider activities that lead to improvement and, conversely, the elimination of activities that lead to less desirable communities. *Late Seral Sagebrush Steppe* communities likely contain a good abiotic and biotic resource base to work from. While prescribed fire may be used to temporally increase the dominance of bunchgrasses, only carefully managed grazing will prevent a transition to the *Depauperate Late Seral Sagebrush Steppe*.

Depauperate Late Seral Sagebrush Steppe communities are in the most critical state. Site resources, including the dominant bunchgrasses, are present but limited in abundance. Grazing and fire have the potential to cause transitions to one of several other steady states. A key question to be asked of these communities is, “Will any kind of prescribed fire lead to an increase in bunchgrasses?” Also of great concern is the question as to whether there is any way to manage grazing to increase the abundance of bunchgrasses. Concern that grazing of any kind may cause the transition across the successional threshold to the less desirable state, *Brush with Introduced Annual Understory*, is certainly justified.

Sagebrush steppe communities in the *Depauperate Late Seral Sagebrush Steppe* are very susceptible to being replaced by less desirable states dominated by shrub species and introduced weedy species. Once the threshold has been crossed to states that no longer contain the original dominant bunchgrasses, grazing and fire by themselves have lost their potential as effective tools for restoration. Only with the artificial addition and manipulation of available site resources through such practices as seeding, use of herbicides, etc., do they regain their potential as effective tools.

It may be well to remember that the sagebrush steppe functions well in the presence of a disturbance regime and that prescriptions for fire alone or grazing alone are much less likely to be successful than prescriptions inclusive of fire and grazing placed into the context of drought. The appropriateness of carefully considering the impacts of disturbance regimes on future plant community composition seems most critical for *Depauperate Late Seral Sagebrush Steppe* communities.

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INVASIVE EXOTIC PLANTS IN SAGEBRUSH ECOSYSTEMS OF THE INTERMOUNTAIN WEST

David A. Pyke

ABSTRACT

The most pervasive weeds of the sagebrush steppe, namely cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*), pose the greatest immediate threat for converting this vast ecosystem into a near monoculture of exotic annual grasses. Only 3 states (California, Oregon, and Utah) list medusahead as a noxious weed. Most states have elected not to place these species on their state noxious weed lists. The current distribution of cheatgrass far exceeds that of medusahead. Surveys show that cheatgrass occurs or has the potential to occur throughout the sagebrush steppe. Medusahead has become a major problem on clay soils in Oregon, southern Idaho, northern California, north-eastern Nevada, and isolated locations in Washington. Although medusahead has not been collected or seen in Montana, this state should heed the experiences of Nevada and Utah, where recent discoveries remind us that this species is continuing to expand its range. Diverse, undisturbed environments do not always protect sites from invasions. Plastic seed production allows populations to maintain themselves in poor years and to increase in good years. These annuals often expand into the inter-spaces between native plants that were once occupied by biological soil crusts. They also produce large amounts of litter that decompose slowly, thus providing a site for their own seed banks to build and for wildfire fuel. Unfortunately, many areas of the sagebrush steppe have not seen the end of weed invasions. A survey of the literature revealed at least 46 exotic species that are commonly viewed as weeds and are capable of sustaining populations in sagebrush ecosystems. Of these, I classified 20 species as highly invasive and competitive. They possess traits that may allow them to successfully establish and sustain viable populations should seeds be introduced into diverse native sagebrush communities, even without human-caused disturbances. Managers should take precautions to halt the further spread of these species on their lands.

INTRODUCTION

The genus *Artemisia* L. (sagebrush) is estimated to have once occupied between 39 and 57 million ha of land in the Intermountain West of the USA (Tisdale et al. 1969, Chadwick 1989). Much of this land is described as semiarid and is dominated by one of four subspecies of big sagebrush (*A. tridentata*) (Shultz 1986, Rosentreter and Kelsey 1991). West (1983a,b) describes two major sagebrush ecosystems that occur in the Intermountain West. In the northern portion of the region, the plant communities exhibit a shared dominance between sagebrush and perennial grasses. The plant communities in the southern portion are dominated by sagebrush, with herbaceous species forming a subdominant role.

Before European settlement, fire was an important environmental (lightning-caused) and human-induced (Native American-caused) force that temporarily drove these ecosystems toward perennial grass dominance. During the intervals between fires, succession allowed shrub recovery. Fires would typically occur every 20 to 100 years, with intervals being shorter in the wetter, more productive mountain big sagebrush (*A. t. ssp. vaseyana*) communities and longer in the drier Wyoming big sagebrush (*A. t. ssp. wyomingensis*) communities (Miller et al. 1994).

The advent of European settlement in the Intermountain West began in the mid-1800s. During the first 60 years, a combination of overgrazing by livestock and introductions of competitive exotic plants set the stage for dramatic changes in plant communities (Miller et al. 1994). Invasive exotic plants, such as cheatgrass, spread quickly across the Intermountain West during the first 100 years after European settlement (Mack 1981, 1986). On Bureau of Land Management (BLM) lands in the Intermountain West, cheatgrass and medusahead now dominate or threaten to dominate over 30 million ha (Pellant and Hall 1994).

Some invasive exotic plants are so common in the Intermountain West that many states do not include these species on their noxious weed lists (Table 1). In sagebrush communities, exotic annual grasses provide sufficient fine fuels to reduce the fire-return intervals and eliminate fire-sensitive native shrubs (West 1983a,b). Although these annual grasses have made significant changes to sagebrush ecosystems, there is no guarantee

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that the annual grass communities they became have stabilized. Other invasive exotic plants such as yellow starthistle (*Centaurea solstitialis*) may replace the annual grasses in some locations (Sheley et al. 1999).

In the U.S. National Strategy for Invasive Plant Management, the first national goal is the effective prevention of the spread of invasive plants (FICMNEW 1997). To achieve this goal, people must understand and educate others on how invasive plants spread and establish in ecosystems. In this paper, I will provide an overview of the exotic plants with disturbance or invasive traits that either currently exist in or have the potential to invade these sagebrush ecosystems. I will examine traits and mechanisms of invasive exotic annual grasses that allow invasion and dominance in sagebrush ecosystems.

OVERVIEW OF EXOTIC INVASIVE PLANTS IN SAGEBRUSH ECOSYSTEMS

The influx of Europeans into the Intermountain West in the middle 1800s soon brought introductions of European plants. Settlement of the region required the production of agricultural commodities for subsistence and exchange among settlers. Miller et al. (1994) illustrated the fortuitous nature of the timing of settlement in this region. The Little Ice Age ended in the middle 1880s. The climate began to warm and precipitation was above normal. Settlement occurred between two major drought cycles, the 1840s and 1930s. Therefore, farming and ranching practices in the region were likely more successful during this period than if they had begun at another time. This success led to expansion of farming throughout the region.

Many of the early introductions of invasive exotic plants into the region occurred through crop seed contamination or through attachment on or ingestion and defecation by livestock. During the late 1800s, unplowed sagebrush lands had collections or notations of exotic invasive plants such as quackgrass (*Elytrigia repens* var. *repens*), redstem filaree (*Erodium cicutarium*), black mustard (*Brassica nigra*), rape mustard (*Brassica rapa*), shepherd's purse (*Capsella bursapastoris*), lambs-quarters (*Chenopodium album*), horehound (*Marrubium vulgare*), cowcockle (*Vaccaria hispanica*), and several annual *Bromus* species, including cheatgrass (Mack 1986, Yensen 1981).

Livestock numbers in the Intermountain West peaked in the early 1900s (Young et al. 1976). Not only were the densities of animals high, but they were present throughout the entire year. This led to widespread overgrazing throughout the region (Griffiths 1902). As forage became scarce, livestock managers even set fires to eliminate fire-sensitive shrubs such as big sagebrush in the hopes of increasing the herbaceous component (Pechanec and Hull 1945). The early surveys of range condition noted increases in exotic annual *Bromus*

species in several locations; however, the suspected problem species were soft brome (*B. mollis*) and cheat (*B. secalinus*) (see references in Mack 1986).

By the drought of the 1930s, the sagebrush ecosystems had undergone numerous introductions of exotic and decreases of native species in many locations. Beginning as early as the 1920s, many dry-land farmers in the region went bankrupt and abandoned their farms (Yensen 1981). The void left by land abandonment and by overgrazing was quickly filled by common ruderal species from Europe and Asia that originally arrived with the crop seeds and were often spread through the distribution of that seed. Russian thistle (*Salsola kali* ssp. *tragus*), flixweed (*Descurainia sophia*), and tumbled mustard (*Sisymbrium altissimum*) became prominent during this time period. The enactment of state and federal seed laws, such as the Federal Seed Act of 1939, helped reduce the transport and spread of exotic species listed as noxious weeds. Many species, like cheatgrass, had already reached their current range by the time these laws were passed; but for others with only isolated introductions, these laws have no doubt slowed their spread.

Many of the exotic plants found in sagebrush ecosystems require continued disturbance of the soils or plant community to sustain their existence. Halting the disturbance and allowing recovery of the native vegetation is often all that is necessary to reduce or eliminate many of the exotics. In Table 1, I suggest that the non-bold species require some form of disturbance to maintain their dominance within sagebrush ecosystems. Plants like halogeton (*Halogeton glomeratus*) and Russian thistle fit this category. They both require disturbance to maintain dominance, but recovery of native plants or revegetation with desirable plants provides the necessary competition or changes in nutrient status to shift the dominance away from the exotic plant (McLendon and Redente 1991, Whitson et al. 1996).

For other exotics, disturbances such as fire may stimulate germination from the seed bank or cause heavy reproduction immediately after fire, thus allowing them to become temporarily prominent in the community. Examples of species in this category include some of the annual mustards, such as flixweed and tumbled mustard. Heavily grazed and trampled locations may also favor some species, e.g., bur buttercup (*Ranunculus testiculatus*).

I consider those species shown in Table 1 in bold as highly invasive and capable of dominating a site once they are introduced. Within sagebrush ecosystems, we have several species that fit each of the three phases of the invasion process: introduction, colonization, and naturalization (Groves 1986). Establishment and maintenance of these species in sagebrush ecosystems is more dependent on the initial introduction of seed than on disturbance. Some plants are expanding their range to



new locations and, therefore, would represent the “introduction” phase of invasion (Groves 1986). These include yellow starthistle, squarrose knapweed (*Centaurea triumfettii*), Mediterranean sage (*Salvia aethiopis*), dyer’s woad (*Isatis tinctoria*), and medusahead. They may dominate local sites in portions of states but continue to be discovered in new locations (Table 1).

The colonization phase (Groves 1986) is represented by species that are already found throughout the Intermountain West. These may be locally dense in certain regions of a state but only sparsely represented in other locations. Examples of species that fit this description include leafy spurge (*Euphorbia esula*), whitetop (*Cardaria pubescens*), and some species in the knapweed complex – diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*C. biebersteinii*). These species are expanding their populations where they currently exist while continuing to spread to new locations.

Within the sagebrush ecosystems, however, the annual exotic grasses exemplify the “naturalization” phase of invasions (Groves 1986) and are the most problematic for management within the region. Species within this group include cheatgrass, Japanese brome (*Bromus japonicus*), and soft brome. These species have attained their geographic distribution in the region. They are now commonly found mixed with native species, even in locations undisturbed by livestock (Svejcar and Tausch 1991, Kindschy 1994). These species are so prevalent throughout the region that it would be difficult or economically burdensome for people to control them; therefore, they are not listed as state or federal noxious weeds.

ANNUAL EXOTICS: MECHANISMS TO INVADE AND DOMINATE

A plant invader that achieves the three phases of the invasion process – introduction, colonization, and naturalization (Groves 1986) – will be widespread in the ecosystem. A combination of both the invader’s traits and the ecosystem’s conditions allows for species to successfully move through the phases of an invasion. However, generalized characteristics of either the species or its potential new environment that would help predict invasions have often led to more exceptions than general rules (Lodge 1993). Since cheatgrass and medusahead are prevalent throughout the sagebrush ecosystems (e.g., Pellant and Hall 1994), I will concentrate my discussion of mechanisms for invasion and dominance on the characteristics of these species, coupled with the characteristics of the ecosystem.

The original introductions of both species into the sagebrush ecosystems likely occurred in the late 1800s. The cheatgrass introduction was probably associated with the import of contaminated cereal grain seed, since the earliest collections were found around wheat-growing areas (Mack 1986). Less is known about the original introductions of medusahead. The earliest collections

occurred near Roseburg, Oregon, between 1884 and 1887 (Furbish 1953, Turner et al. 1963). The first collection in the Intermountain West occurred near Steptoe Butte, Washington (St. John 1937). One could argue that contaminated cereal grain seed was to blame for the Washington introduction since this was a wheat-growing region, but others have speculated that the seed was introduced on the fur of imported animals (Hilken and Miller 1980).

Cheatgrass is currently more prevalent than medusahead in sagebrush ecosystems. Mack (1981) estimated the complete range of cheatgrass in the Intermountain West at 40 million ha (99 million acres). This estimate is probably conservative, since Pellant and Hall (1994) surveyed BLM lands and estimated that one million ha (2.5 million acres) of these lands in Idaho, Nevada, Oregon, Utah, and Washington are dominated by cheatgrass (>60% of the species composition by weight). They estimated that 31.8 million ha (78.5 million acres) of BLM lands (about 80% of these lands in the 5 states) have the potential for cheatgrass to become dominant.

Although medusahead was introduced at about the same time as cheatgrass, it has spread more slowly than cheatgrass. Miller et al. (1999) estimated that medusahead occurs on 400,000 ha (988,000 acres) throughout its complete range; however, much of that land is in California. Pellant and Hall’s (1994) survey of BLM lands in the Intermountain West estimates that medusahead occupies approximately 167,000 ha (412,500 acres) in Idaho and Oregon. This species has not reached its potential distribution in the region since new introductions have been reported in several locations in Utah and Nevada (Horton 1991, Young 1992).

The difference between cheatgrass and medusahead in rate of spread may relate to their genetics. Both species have self-mating reproductive systems. We know very little about the genetics of medusahead, but we know that several genetic strains of cheatgrass from different regions of Eurasia have been introduced into the Intermountain West (Novak et al. 1991, Novak and Mack 1993, Pyke and Novak 1994). These multiple cheatgrass introductions may provide greater adaptations to establish and survive in a wider range of environments. Future research might investigate whether medusahead’s slow expansion relates to less genetic diversity in the form of fewer introductions from its native environment.

INVASION MECHANISMS

Both cheatgrass and medusahead are obligate annual grasses (only rare exceptions have been noted [Harris 1967]); therefore, population sustainability, as well as population initiation, requires available seeds. The invasion process of an annual plant requires the combination of seed arrival to the site (dispersal dynamics) plus germination and survival of the plant until successful



reproduction (Cousens and Mortimer 1995). To understand how these species invade the sagebrush ecosystem, we must understand their seed production and dispersal.

Both cheatgrass and medusahead are highly plastic in their production of seeds. Under a wide range of environmental conditions (Rice and Mack 1991), most individuals will produce at least one seed. To exemplify this point, one-month-old plants can withstand weekly severe grazing (defoliation to the soil surface) and still produce viable seeds if given time to reproduce (eight weeks) at the end of the growing season (Pyke 1987). Both species have indeterminate reproduction on their inflorescences, an advantage in variable environments (Pyke 1986) that allows for a wide range in seeds per tiller. The number of tillers produced per plant also contributes to the total seed production per individual and tends to be regulated by the density of the neighboring plants. Tiller production generally varies between 1 and 25 tillers per individual for dense vs. sparse neighborhoods (Hulbert 1955, Miller 1996). In a fertile yet sparse system, Sharp et al. (1957) reported a medusahead plant produced 133 tillers.

The neighborhood of species that grow with these annuals also influences their reproduction. Reichenberger and Pyke (1990) showed that reproduction of cheatgrass declined, depending on the species of the neighbor (sagebrush [3.6 cheatgrass seeds/plant] < bluebunch wheatgrass [*Pseudoroegneria spicata*] [6.1 seeds/plant] < desert crested wheatgrass [*Agropyron desertorum*] [8.1 seeds/plant]).

The soils on which plants grow may contribute to their success. Young (cited in Miller et al. 1999) speculates that medusahead has not been found in many Nevada locations because the salt desert communities in the valleys and the coniferous forests in the mountains act as barriers for establishment. Miller (1996) found medusahead reproduction at a site with clay soils was higher than medusahead on loam soil; however, climate may have also contributed to this result.

The variable yet temporally constant seed production of these annual grasses provides the necessary base resource for invasion to occur. The dispersal of seed to new locations is the next component that contributes to invasion success. Both species have similar mechanisms for long- and short-distance dispersal. I previously mentioned the speculation that both animal transport and crop seed contamination are likely avenues for the original introductions. These mechanisms are potential sources for continued spread.

Although regulations have curtailed the spread of many invasive plants with crop seeds, care must be taken to ensure the purity of seeds used in revegetation, restoration, or rehabilitation projects. Since many people desire native seeds on such projects, seeds are often collected in the wild, making the project vulnerable

to contamination by nontarget seeds. Care should be taken to request that seed not contain invasive weeds like cheatgrass (Table 1) and to have a professional seed lab check purity prior to seeding.

Animal transport of invasive-plant seeds has been documented in many species. Although animal transport is likely in cheatgrass and medusahead, clear documentation of it has not been reported. The barbed awns of both species make them suitable for transport on animal fur. Many review papers have speculated about sheep or livestock in general as the dispersal vectors for these species (Mack 1981, Yensen 1981, Young 1992), but no studies have attempted to quantify this.

Recreational activities may result in seed dispersal. Seed transport on clothing is a common occurrence in sites with mature cheatgrass. The seeds become lodged in clothing, such as socks or shoes, and are moved along with the people. It is also common for seeds to become lodged in the chassis' of automobiles and all-terrain vehicles. In all cases, seeds may not dislodge until they have moved hundreds of miles.

The mechanisms for short-distance dispersal in both species involve secondary dispersal by wind once the seeds drop from the plant. Single spikelets of cheatgrass or whole inflorescences of medusahead are often blown across the soil until they hit an obstruction (e.g., litter or soil crack) (Turner et al. 1963, Bookman 1983).

The last component of an introduction is the plant's ability to germinate, emerge, and survive in the environment in which it is now found. The ability for cheatgrass to emerge in almost any season, provided there is adequate moisture (Mack and Pyke 1984), and to maintain high survival and reproduction even under intense and frequent herbivory (Pyke 1986, 1987) provides this species with an excellent mechanism to invade. Medusahead appears more restricted by soil texture and precipitation. It is more successful on clay than on loam soils (Young 1992, Miller 1996). It also seems to require more moisture than cheatgrass to successfully reproduce (Miller et al. 1999). These requirements tend to restrict it to clay soils with >30 cm of annual precipitation.

DOMINANCE MECHANISMS

The mechanisms that provide an introduction advantage to cheatgrass and medusahead in sagebrush ecosystems are generally the same types of mechanisms that confer an introduction advantage to other species. However, the combinations of mechanisms that allow these species to dominate the sagebrush ecosystems are more specific to these species, or at least to annual grasses in general, than the introduction mechanisms. Cheatgrass and medusahead become dominant in this ecosystem because of three general mechanisms. First, they are capable of occupying spatial or temporal niches that other vascular species commonly do not occupy. Second, they are capable of tolerating or avoiding



disturbances that negatively impact many native plants in the ecosystem. Third, they compete successfully for resources with other vascular plant species in the ecosystem.

Spatially, these annual grasses occupy and expand to fill the interspaces between vascular plants. Nonvascular plants that make up the biological soil crust, such as mosses, lichens, algae, and cyanobacteria, historically occupied these interspaces. Biological soil crusts are easily damaged by trampling, especially when they are dry (Harper and Marble 1988, West 1990). Although one study has indicated that biological soil crusts may reduce cheatgrass establishment (Larsen 1995), others have shown that these crusts can enhance establishment, even with exotic plants (Harper and Marble 1988). Further research is needed to investigate the role of these crusts in vascular plant establishment.

Annual grasses are capable of establishing in a wide range of spatial locations. Cheatgrass seeds and seedlings appear to exist and grow under shrub canopies and in the interspaces (Young and Evans 1975). Soil cracks and seed burials to depths up to 2.0 cm are equally safe sites for emergence (Bookman 1983). Litter, especially from itself (Young et al. 1971), enhances medusahead germination.

Temporally, these annual grasses are capable of germinating in either the autumn, winter, or spring (Young 1992). Root growth of both annuals is quicker than bluebunch wheatgrass, a common dominant native grass (Harris and Wilson 1970, Harris 1977). This faster growth allows the annuals to establish their root systems before the natives. Bookman and Mack (1982) have shown that cheatgrass is capable of adjusting the placement of its roots, depending on the root placement of its neighbor. This plasticity in root placement may confer an advantage to cheatgrass when initially establishing in a community. Both annual grasses are able to capture nutrient pulses as they occur in the sagebrush ecosystem. Phenologic differences between these species allow cheatgrass to benefit more from early season pulses, while medusahead benefits from late season pulses (Bilbrough and Caldwell 1997).

The dominance of invasive exotic annual grasses in sagebrush ecosystems is related to the annuals' efficient mechanisms for withstanding disturbances to the ecosystem by livestock grazing and fire. Medusahead and cheatgrass are thought by many to use different mechanisms (avoidance for medusahead and tolerance for cheatgrass) when confronted with livestock grazing; however, research results are mixed regarding grazing avoidance yet clearly support the grazing tolerance hypothesis (as defined by Briske 1991).

Nutritionally, both cheatgrass and medusahead provide similar moisture content, crude protein, crude fat and fiber, and lignin content to that of desirable grasses,

but medusahead is high in silica. Based upon this high silica content, Bovey and others (1961) concluded that medusahead was unpalatable to livestock at all growth stages. However, the only grazing experiment indicated that sheep used the plant when it was green (Lusk et al. 1961). Other studies have calculated the impact on livestock grazing using the compositional proportion of medusahead in the plant community, but actual grazing evaluations that show non-use or preferences do not appear in the literature (Higgins and Torell 1960, Torell et al. 1961). If medusahead's silica content provides an avoidance mechanism, this may occur when litter becomes deep, causing livestock to avoid the plant, as Hironaka speculated (cited in Hilken and Miller 1980).

Regardless of the potential for medusahead to avoid grazing, cheatgrass clearly is tolerant of grazing (Pyke 1986, 1987). Cheatgrass exhibits typical morphological characteristics of grazing-tolerant plants that allow them to regrow following defoliation (Archer and Pyke 1991). Using livestock to control cheatgrass has been reported in one review, but it notes that grazing must be continued until plants reach the purple stage and must be repeated for several years (Mosley 1996). However, Daubenmire (1940) noted that if grazing is not continued, cheatgrass would quickly return.

Fire is a natural disturbance in the sagebrush ecosystem, but the introduction of exotic annual grasses has shortened fire cycles and led to a reduction in the shrub component (D'Antonio and Vitousek 1992). Before the introduction of exotic annual grasses, the natural fire-return intervals were thought to be between 20 and 100 years, depending on the local climate and subspecies of sagebrush (Burkhardt and Tisdale 1976, Wright and Bailey 1982). Now, with annuals like cheatgrass in the ecosystem, the return interval has shortened to as few as five years under some conditions (Whisenant 1990). Similar to cheatgrass, medusahead provides fine fuels for wildfires, and the annual life span of both species results in large amounts of dry litter available to burn during the late summer (Young et al. 1971, Whisenant 1990). For medusahead, prescribed fire has been successfully used as a temporary control measure before revegetation (Miller et al. 1999). The ultimate result of frequent fires in sagebrush ecosystems is the elimination of fire-sensitive shrubs such as sagebrush (West 1983a,b).

The last mechanism of cheatgrass and medusahead that contributes to their eventual dominance in sagebrush ecosystems is their ability to compete successfully with native plants for available nutrients and water. The early germination and rapid root growth of both species are thought to contribute to this ability (Harris 1967, Harris and Goebel 1976, Harris 1977). The competitive advantage of these exotic annual grasses is most apparent when they compete with seedlings, even with competitive introduced forage grasses (Aguirre and Johnson 1991, Francis and Pyke 1996).



Since cheatgrass and medusahead overlap in their distribution, they do compete for resources in those locations. Controlled experiments have yielded mixed results regarding the competitive outcomes of mixed populations of medusahead and cheatgrass. In low-nutrient environments, either medusahead excelled or the two species were similar; but under high nitrogen levels, cheatgrass was most successful (Dakheel et al. 1993). Climate and soils may control the success of one species over the other where they coexist. Medusahead tends to dominate clay soils with more than 30 cm precipitation, whereas cheatgrass dominates coarser-textured soils in drier climates (Dakheel et al. 1993, Miller et al. 1999).

CONCLUSIONS

There is no guarantee that the exotic plants of today are the only species with which managers of sagebrush ecosystems must contend. Preventing further spread of exotic plants will require a concerted effort on the part of land managers and land users alike. They must consider the various modes of introductions for these species and use precautionary measures when moving throughout the region. Despite their best efforts, invasive exotic plants may continue to spread. Therefore, educating the public on the identification of exotic plants and on the plants' modes of introduction, and then applying this knowledge when people use the land, should help to slow the spread of exotic plants and to retain the native ecosystems for future generations to use and enjoy.



Table 1. List of the common weeds, noxious weeds, or invasive exotic plants in sagebrush ecosystems of the Intermountain West. The growth form (herb, shrub, or grass), life history strategy (annual, biennial, or perennial), the origin of the plant, states within the Intermountain West where it is listed as a noxious weed, and comments on the geographic distribution within the region are given for each species (Whitson et al. 1996, Rice 1997, Shelley and Petroff 1999, USD, NRCS 1999). Those species listed in bold are highly invasive and competitive in sagebrush ecosystems.

Family	Species	Common Name	Growth Form	Life History	Origin	Noxious	Distribution
Asteraceae	<i>Acroptilon repens</i> (L.) DC. [formerly <i>Centaurea repens</i> L.]	Russian knapweed	herb	perennial	Eurasia	CA, ID, MT, NV, OR, UT, WA, WY	Locally dense throughout Northwest
Asteraceae	<i>Arctium minus</i> Bernh.	common burdock, lesser burdock	herb	biennial, perennial	Europe	NV, WY	Widespread
Asteraceae	<i>Carduus acanthoides</i> L.	spiny plumeless thistle	herb	biennial, perennial	Eurasia	CA, WA, WY	Locally dense in ID, MT, WA, & WY
Asteraceae	<i>Carduus nutans</i> L.	musk thistle, nodding plumeless thistle	herb	biennial, perennial	Eurasia	CA, ID, NV, OR, UT, WA, WY	Widespread
Asteraceae	<i>Carthamus lanatus</i> L.	distaff thistle	herb	annual	S. Europe, N. Africa	CA, OR	Occasionally in CA, OR, & NV
Asteraceae	<i>Centaurea biebersteinii</i> DC. [formerly <i>Centaurea maculosa</i> Lam.]	spotted knapweed	herb	biennial, perennial	Eurasia	CA, ID, MT, NV, OR, UT, WA, WY	Widespread
Asteraceae	<i>Centaurea diffusa</i> Lam.	diffuse knapweed	herb	annual, perennial	Eurasia	CA, ID, MT, NV, OR, UT, WA, WY	Widespread
Asteraceae	<i>Centaurea iberica</i> Trev. ex Spreng.	Iberian starthistle	herb	annual, biennial	Europe	CA, NV, OR	Locally dense in WA, OR, CA, & WY
Asteraceae	<i>Centaurea solstitialis</i> L.	yellow starthistle	herb	annual	Europe	CA, ID, MT, NV, OR, UT, WA	Locally dense in OR, WA, ID, CA & NV
Asteraceae	<i>Centaurea triumfettii</i> All. [formerly <i>C. virgata</i> Lam.]	squarrose knapweed	herb	perennial	Europe	CA, OR, UT	Locally dense in UT, OR, CA
Asteraceae	<i>Chondrilla juncea</i> L.	rush skeletonweed, hogbite	herb	perennial	Eurasia	CA, ID, MT, OR, WA	Locally dense throughout Intermountain West
Asteraceae	<i>Cirsium arvense</i> (L.) Scop.	Canadian thistle	herb	perennial	Eurasia	CA, ID, MT, NV, OR, UT, WA	Widespread
Asteraceae	<i>Crepina vulgaris</i> Cass.	common crupina	herb	annual	Eurasia, N. Africa	CA, ID, MT, OR, WA, USA	Locally dense in CA, ID, OR, WA



Table 1 (Cont.)

Family	Species	Common Name	Growth Form	Life History	Origin	Noxious	Distribution
Brassicaceae	<i>Brassica nigra</i> (L.) W.D.J. Koch	black mustard	herb	annual	Europe		Widespread
Brassicaceae	<i>Brassica rapa</i> L.	rape mustard	herb	annual, biennial	Europe		Widespread
Brassicaceae	<i>Capsella bursa-pastoris</i> (L.) Medik.	shepherd's purse	herb	annual	Europe		Widespread
Brassicaceae	<i>Cardaria pubescens</i> (C.A. Mey.) Jarmolenko	whitetop	herb	perennial	Eurasia	CA, OR, UT, WA, WY	Widespread
Brassicaceae	<i>Descurainia sophia</i> (L.) Webb ex Prantl	flixweed, herb sophia	herb	annual, biennial	Europe		Widespread
Brassicaceae	<i>Isatis tinctoria</i> L.	dyer's woad	herb	biennial, perennial	Europe	CA, ID, MT, NV, OR, UT, WA, WY	Locally dense in ID, MT, UT, WY, NV, CA
Brassicaceae	<i>Lepidium latifolium</i> L.	perennial pepperweed, tall whitetop	herb	perennial	Eurasia	CA, ID, NV, OR, UT, WA, WY	Locally dense, transitions from meadow to upland
Brassicaceae	<i>Sisymbrium altissimum</i> L.	tumble mustard	herb	annual, biennial	Europe		Widespread
Brassicaceae	<i>Thlaspi arvense</i> L.	field pennycress	herb	annual	Europe		Widespread
Caryophyllaceae	<i>Gypsophila paniculata</i> L.	baby's breath	herb	perennial	Europe	CA, WA	Locally dense in ID, MT, WA, & OR
Caryophyllaceae	<i>Vaccaria hispanica</i> (P. Mill.) Rauschert	cowcockle, cow soapwort	herb	annual	Europe		Widespread
Chenopodiaceae	<i>Chenopodium album</i> L.	lambsquarters	herb	annual	Eurasia		Widespread
Chenopodiaceae	<i>Halogeton glomeratus</i> (Bieb.) C.A. Mey.	halogeton	herb	annual	Asia	CA, NV, OR	Widespread, alkaline soils
Chenopodiaceae	<i>Salsola kali</i> L. ssp. <i>tragus</i> (L.) Celak.	Russian thistle	herb	annual	Eurasia		Widespread
Clusiaceae	<i>Hypericum perforatum</i> L.	common St. John's wort, klamathweed	herb	perennial	Europe	CA, MT, NV, OR, WA	Widespread
Dipsacaceae	<i>Dipsacus fullonum</i> L.	Fuller's teasel, common teasel	herb	biennial, perennial	Europe		Widespread



Table 1 (Cont.)

Family	Species	Common Name	Growth Form	Life History	Origin	Noxious	Distribution
Euphorbiaceae	<i>Euphorbia esula</i> L.	leafy spurge, wolf's milk	herb	perennial	Eurasia	CA, ID, MT, NV, OR, UT, WA, WY	Widespread
Geraniaceae	<i>Erodium cicutarium</i> (L.) L'Her. ex Ait.	redstem filaree, redstem stork's bill	herb	annual, biennial	Eurasia		Widespread
Lamiaceae	<i>Marrubium vulgare</i> L.	horehound	herb, subshrub	perennial	Europe		Widespread
Lamiaceae	<i>Salvia aethiopis</i> L.	mediterranean sage	herb	biennial	S. Europe, N. Africa	CA, NV, OR, WA	Locally dense in OR, also found in WA, ID, CA
Poaceae	<i>Aegilops cylindrica</i> Host	jointed goatgrass	grass	annual	Europe	CA, ID, OR, WA	Locally dense in MT, eastern WA often associated with winter wheat
Poaceae	<i>Bromus japonicus</i> Thunb.	Japanese brome	grass	annual	Europe		Widespread
Poaceae	<i>Bromus mollis</i> L.	soft brome	grass	annual	Europe		Widespread
Poaceae	<i>Bromus rubens</i> L.	red brome, foxtail brome	grass	annual	Europe		Locally dense in CA, ID, NV, OR, UT, WA
Poaceae	<i>Bromus secalinus</i> L.	cheat, rye brome	grass	annual	Europe		Widespread
Poaceae	<i>Bromus tectorum</i> L.	cheatgrass, downy brome	grass	annual	Eurasia		Widespread
Poaceae	<i>Poa bulbosa</i> L.	bulbous bluegrass	grass	perennial	Europe		Widespread
Poaceae	<i>Taeniatherum caput-medusae</i> (L.) Nevski	medusahead	grass	annual	Eurasia	OR	Locally dense in CA, ID, NV, OR, and WA
Poaceae	<i>Ventenata dubia</i> (Leers) Coss. & Durieu	ventenata	grass	annual	Eurasia		Locally dense in N. ID, E. WA and N.E. OR
Ranunculaceae	<i>Ranunculus testiculatus</i> Crantz	bur buttercup	herb	annual	Eurasia		Widespread
Scrophulariaceae	<i>Linaria dalmatica</i> ssp. <i>dalmatica</i> (L.) P. Mill.	Dalmatian toadflax	herb	perennial	SE Europe	CA, ID, MT, OR, WA, WY	Locally dense throughout Northwest
Scrophulariaceae	<i>Linaria vulgaris</i> P. Mill.	butter-and-eggs, yellow toadflax	herb	perennial	Eurasia	ID, OR, WA, WY	Scattered throughout Northwest
Scrophulariaceae	<i>Verbascum thapsus</i> L.	common mullein	herb	biennial, perennial	Europe	WA	Widespread



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STRUCTURE AND FUNCTION OF BIOLOGICAL SOIL CRUSTS

Jayne Belnap

INTRODUCTION

In arid and semiarid lands throughout the world, the cover of vegetation is generally sparse or absent. Open spaces between the higher plants are not bare of autotrophic life but usually covered by a community of highly specialized organisms. This soil surface floral community consists of cyanobacteria, green algae, lichens, mosses, microfungi, and other bacteria. Cyanobacterial and microfungi filaments weave throughout the top few millimeters of soil, gluing loose soil particles together to form a biological crust. These crusts occur in all hot, cool, and cold arid and semiarid regions. They may constitute up to 70% of the living cover (Belnap 1994) and have only recently been recognized as having a major influence on terrestrial ecosystems. These communities are also referred to as cryptogamic, cryptobiotic, microbial, or microphytic soil crusts (Harper and Marble 1988).

Physical soil crusts are also a major structural feature in many arid regions and are often confused with biological soil crusts. Most physical crusts are formed by raindrops hitting unprotected soil surfaces, which breaks apart surface aggregates. Smaller particles then wash into spaces between larger particles, thus clogging soil pores and reducing infiltration rates by as much as 90%. In general, rain-formed crusts are less than 5 mm thick. This layer is often harder than the rest of the soil because it is drier and compounds such as salts, lime, and silica are often deposited at the surface as water evaporates. With large pores absent, these crusts increase water runoff and soil erosion and prevent the emergence of seedlings. Thus, physical crusts play a very different role in arid ecosystems than do biological crusts (Lemos and Lutz 1957).

MICROSTRUCTURE

Lichens and mosses are easily seen without aid of magnification. However, much of the structure and function of crusts depends on cyanobacteria, green algae, and microfungi, which are often too small to be seen without a microscope. In most desert soils, cyanobacteria contribute the most to crust microstructure.

Cyanobacterial filaments confer structural integrity to the soils in which they occur. When wetted, the sheath of filamentous cyanobacteria swell, expelling the living filaments and leaving behind empty sheath material. These filaments often string sand and clay particles together, much like fibers in fiberglass. Depending on environmental conditions and soil textures, cyanobacterial sheaths may be found at depths of 10 cm below the soil surface (Belnap and Gardner 1993). As aeolian and water-borne materials are trapped in the polysaccharide sheaths of cyanobacteria on the soil surface, old sheaths are gradually buried. Thus, influence on water-holding capacity and soil stability may extend far below the depth to which light can penetrate, unless sheaths are crushed. If sheath-soil connections are broken by trampling or vehicles, these sheaths are no longer living and therefore cannot be repaired.

ECOLOGICAL ROLES – CARBON AND NITROGEN FIXATION

Biological soil crusts are an important source of fixed carbon on sparsely vegetated areas throughout the West (Beymer and Klopatek 1991). While vascular plants provide organic matter to soils directly underneath them, large interspaces between plants have little opportunity to receive such input. Carbon contributed by soil crusts helps keep plant interspaces fertile and thus provides energy sources for other microbial populations.

The dominant components of biological soil crusts are photosynthetic organisms that require sunlight. When soils are dry, the bulk of the cyanobacterial biomass is at 0.2 - 0.5 mm, with bundles found down to 4 mm where sufficient light for net carbon gain is available but UV exposure is reduced (Garcia-Pichel and Belnap 1996). Carbon fixation rates are dependent on moisture and temperature (Rychert et al. 1978; Nash et al. 1982a,b; Lange et al. 1997). Most crustal species increase photosynthetic rates with increasing temperatures up to about 26-28°C, after which rates decline.

Nitrogen concentrations are known to be low in desert ecosystems relative to other ecosystems. Total atmospheric input of nitrogen over the past 10,000 years has been conservatively estimated at about 3 kg/m² (ignoring cyanobacteria inputs), with 77% lost through wind erosion, ammonia volatilization, nitrification, and denitrification (Peterjohn and Schlesinger 1990).

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Extensive surveys in cold deserts have revealed only a few nitrogen-fixing plants (Farnsworth et al. 1976). As nitrogen can limit net primary productivity in many desert ecosystems, normal nitrogen cycles are critical to the fertility of semiarid soils and in preventing desertification (Dregne 1983).

Cyanobacteria and cyanobacterial-containing soil lichens can be an important source of both fixed nitrogen for plants and soils in desert ecosystems (Evans and Ehleringer 1993, Belnap 1995). Nitrogen inputs from biological soil crusts have been estimated from 1 to 100 kg/ha annually (Harper and Marble 1988), with the lowest estimates still almost 10 times atmospheric input estimates. Nitrogen fixation is highly dependent on past and present water and light regimes, as well as species composition (Rychert et al. 1978, Belnap 1996), with maximum fixation at approximately 26°C and above 20% moisture. Past disturbance history is also a critical factor in determining fixation rates (Belnap 1995, 1996).

Five to 88% of N fixed by *Nostoc* has been shown to leak into the surrounding substrate (Magee and Burris 1954, Belnap et al. 1997). Nitrogen leaked from these organisms is available to nearby vascular plants (Mayland and MacIntosh 1966). Vascular plants growing in biologically crusted areas show higher tissue concentrations of nitrogen when compared to plants in uncrusted soils (Harper and Pendleton 1993; Belnap 1994, 1995; Belnap & Harper 1995). As with carbon, crusts contribute nitrogen to soils both under plants and in plant interspaces, thereby counteracting the tendency of nutrients to concentrate around perennial plants.

EFFECTS ON VASCULAR PLANTS

Germination and establishment: The presence of crusts can affect vascular plant germination and establishment. While small cracks and crannies on the soil surface are sufficient for small-seeded plants to lodge and germinate, most large-seeded plants need some cover by soil or vascular plant litter. In deserts where plant litter is often limiting in interspaces, large native seeds generally have self-burial mechanisms (such as hygroscopic awns) or are rodent-cached. Plants adapted to loose, moving soils (such as sand dunes) or deep litter (forests) accomplish this passively. However, exotic species may lack such adaptations. As crusts stabilize soils, germination can be inhibited in sites with well-developed crusts and low plant litter, as was recently demonstrated for the annual exotic cheatgrass (*Bromus tectorum*), in both the field and the laboratory (Kaltenecker 1997). Once the seeds germinate, biological soil crusts show no barrier to seedling root penetration (J. Belnap, USGS Biological Resources Division, and R.L. Pendleton and S.E. Meyer, USDA Forest Service Shrub Sciences Laboratory, unpublished data). Seedling germination *per se* has not been shown to limit species density or presence in desert plant communities. Rather, many studies worldwide

suggest that vascular plant cover is most often controlled by water and/or nutrient availability rather than other site factors (Mabbutt and Fanning 1987, Tongway and Ludwig 1990, Dunkerley and Brown 1995).

A recent review of the literature regarding the survival and biomass of plants in crusted soils compared to uncrusted soils shows that all perennial plants in cool deserts are either enhanced or not affected by the presence of biological soil crusts (Belnap et al. 2000). This included both fine- and coarse-textured soils. No study showed a negative relationship between crusts and vascular plant growth. Numerous other authors have reported similar findings (reviewed in Harper and Marble 1988). On the other hand, the presence of perennial plants may aid the survival of crustal components by increasing surface moisture due to shading.

Nutrient levels of plants growing on crusted soil generally show higher concentrations and/or greater total accumulation of various essential nutrients when compared to plants growing in adjacent, uncrusted soils. In southeast Utah, leaf tissue nitrogen in annual, biennial, and perennial species was 9 to 31% higher in crusted areas. Dry weights were greater as well (Belnap 1995, Belnap and Harper 1995). This was verified with greenhouse experiments (Harper and Pendleton 1993). Other authors have obtained similar results with other species (Shields and Durrell 1964, Brotherson and Rushforth 1983).

Several mechanisms have been postulated to explain this effect. Crusts accumulate nutrient-rich fine soil and organic matter (Fryberger et al. 1988, Verrecchia et al. 1995). Cyanobacterial sheath material is often coated with negatively charged clay particles. Positively charged macro-nutrients bind to these particles and are thus prevented from leaching from the soil profile (Belnap and Gardner 1993). These clay particles are more nutrient-rich than sand (Black 1968). Compounds in the gelatinous sheath material of cyanobacteria are able to chelate elements essential for their growth, e.g., iron, copper, molybdenum, zinc, cobalt, and manganese (Lange 1974). It is also possible that nutrient differences are a result of a thermal effect, as dark crusts would be warmer than lighter uncrusted soils and uptake of nutrients would occur at a higher rate. Herbivores and other consumers may benefit directly from the enhanced nutrient status of these ecosystems (Belnap and Harper 1995). Indirect effects include positive correlations between soil mycorrhizae and microarthropod populations with the presence of well-developed biological soil crusts (Harper and Pendleton 1993).

WATER RELATIONS

The effect of biological soil crusts on soil water relations is highly variable between different regions, soils, and climatic regimes. Crustal development (e.g., cyanobacterial, lichen, moss), climatic regimes, the



amount of surface roughness, time since destructive disturbance, soil texture, and soil structure can all heavily influence hydrologic cycles at a given site. Soil texture is especially important and can override any effect of biological soil crusts. For instance, soils with high shrink-swell clays have low infiltration rates and sandy soils have high infiltration rates, regardless of the biological soil crusts present.

Results of research conducted under a variety of soil and climate conditions around the world show the variable and interactive effects of biological soil crusts and soil properties. While the presence of the mucilaginous cyanobacteria can decrease soil permeability, increased surface roughness can increase water pooling and residence time. Consequently, in cool and cold deserts, where frost-heaving is common and biological soil crusts greatly increase soil-surface roughness, the presence of biological soil crusts generally increases the amount and depth of rainfall infiltration. In warm deserts, where frost-heaving is not present and biological soil crusts are relatively flat, the influence of crusts on infiltration rates is dependent mostly on soil type, with crusted sandy soils showing a greater relative reduction (though absolute rates are still higher) than crusted fine-textured soils (Warren 2000).

Though overall infiltration of precipitation is critical for plant growth, where the water infiltrates can also be critical in maintaining plant community structure. Recent work done on banded vegetation has shown that water infiltration and runoff patterns can be important in maintaining vegetative community structure in hyper-arid zones. Biological soil crusts cover inter-band soils. When these inter-band biological soil crusts are disrupted, water infiltration increases between vegetated areas. This results in less water reaching the vegetated bands, causing large die-offs. This was also seen in Israel, where vegetation died when water infiltration was increased in plant interspaces (E. Zaady, Ben-Gurion University of the Negev, personal communication).

The effect of biological soil crusts on soil moisture is also variable. Soils under biological soil crusts showed deeper water penetration into the profile and greater availability during drought (Brotherson and Rushforth 1983, Abrahams et al. 1988). The ability of the crust to seal the soil surface and reduce evaporation due to high clay and silt concentrations in the crusts has been repeatedly proposed (Danin 1978, Brotherson and Rushforth 1983, Williams et al. 1995a) and recently supported by research specifically designed to address the issue (Verrecchia et al. 1995). However, this can vary. In Utah and Mexico, soil moisture was less under disturbed crusts than intact crusts (Harper and Marble 1988, Meyer and Garcia-Moya 1989). Increased soil temperature, through the absorption of solar energy by black crusts, may increase soil moisture evaporation rates (Harper and Marble 1988).

SOIL STABILIZATION

Wind and water can be major erosive forces in deserts, as sparse vegetation leaves large soil spaces unprotected by plant litter or vegetative cover (Goudie 1978). Inter-space soils in deserts are most often stabilized by rocks or biological soil crusts. Polysaccharides extruded by the cyanobacteria and green algae, in combination with lichen and moss rhizines, entrap and bind soil particles together, increasing the size of soil aggregates. As soil aggregates get larger, they are heavier, have a greater surface area, and are therefore more difficult for wind or water to move. The presence of biological soil crusts enables otherwise loose, sandy soils to stay in place on steep slopes and stabilizes pockets of very shallow soil (reviewed in Harper and Marble 1988, Belnap and Lange 2000). Globally, many authors have reported that the presence of biological soil crusts reduces soil susceptibility to water erosion through reduced raindrop erosion and sediment loss from sites (Foth 1978, Harper and Marble 1988, Alexander and Calvo 1990, Eldridge 1993, Eldridge and Greene 1994, Ladyman and Muldavin 1994). Biological soil crusts are unambiguously effective in reducing wind erosion of soil. All studies have shown that crust cover reduces wind erosion by requiring much higher wind speeds to initiate soil particle movement (Williams et al. 1995b; McKenna-Neuman et al. 1996; Belnap and Gillette 1997, 1998). Resistance to water and wind erosion parallels biological crust development. The degree to which different types of crusts protect the soil surface from both wind and water erosion is: bare soil < algal crust < lichen/moss crust (Tchoupounou 1989; Kinnell et al. 1990; Eldridge and Greene 1994; Belnap and Gillette 1997, 1998).

EFFECTS OF DISTURBANCE

Many uses of deserts result in impacts to biological soil crusts. The greatest impacts come from off-road vehicles, both military and civilian; trampling by livestock and people; and various mining activities. Effects of these activities are especially noticeable at sites with highly erodible soils with high topographic relief. Surface disturbance generally results in changes in species composition of soil crusts. While multiple species of soil lichens and mosses, as well as 4 or more species of cyanobacteria, can be found in untrampled areas on most soil types, no lichens and only 1 species of cyanobacteria are generally found in directly adjacent trampled areas (Belnap 1995).

Trampled surfaces are generally flat. Flattened surfaces do not slow water or wind velocity, nor does sediment have an opportunity to settle out; thus, more sediment is lost from trampled sites than untrampled sites. Water residence time on smooth surfaces is shorter and water infiltration reduced (Harper and Marble 1988). Trampling breaks cyanobacterial connections, compromising soil stability. Arid soils with little tendency to



form inorganic aggregates (e.g., sandy soils) are more susceptible to stresses when dry, while soils with inorganic crusting are more susceptible to impacts when soils are wet. Soil formation is extremely slow in deserts, taking 5,000 to 10,000 years (Dregne 1983). Compression disturbances to the crusts greatly decrease resistance to wind erosion for all soil types, regardless of the disturbance regime or soil type, as cyanobacteria and lichens are brittle when dry and crush easily. Vehicle tracks result in greater damage than hoof prints on a given soil type. After 10 years of recovery, sandy soils tested in southeast Utah were still susceptible to wind erosion at commonly occurring wind speeds, while fine-textured soils in southern New Mexico showed much quicker recovery (Belnap and Gillette 1997, 1998; Herrick, USDA Agricultural Research Service, and Belnap, USGS Biological Resources Division, unpublished data). Nearby biological soil crusts can also be buried by blowing sediment, resulting in the death of the photosynthetic organisms (Belnap 1995, 1996). Because over 75% of the photosynthetic biomass and almost all photosynthetic productivity are from organisms in the top 3 mm of these soils, very small soil losses can reduce site fertility and soil stability.

Nutrient Cycles: Crust disturbance can result in large decreases in soil nitrogen through a combination of reduced input (Belnap et al. 1994; Belnap 1995, 1996; Evans and Belnap 1999) and elevated losses (Peterjohn and Schlesinger 1990). Reductions in input can continue long after disturbance has been removed: current long-term studies demonstrate a 42% decrease in soil nitrogen and 34% decrease in plant tissue nitrogen 25 years following release from grazing. This has severe implications for ecosystems that are dependent on biological crusts for nitrogen, such as the Colorado Plateau (Evans and Ehleringer 1993, Evans and Belnap 1999). Reduced fertility of systems is one of the most problematic aspects of desertification (Dregne 1983).

Albedo: Albedo is also of concern in semiarid and arid systems. When trampled crusts were compared to untrampled crusts, there was up to a 50% increase in reflectance across the spectrum. This represents a change in the surface energy flux of approximately 40 watts/m². Soil temperatures are up to 14°C lower on the lighter, trampled surface (Belnap 1995). Altered soil temperatures affect rates of carbon and nitrogen fixation; microbial activity; plant germination, growth, and nutrient uptake; and soil water evaporation (Harper and Marble 1988, Bush and Van Auken 1991). Food and other resources are often partitioned among ants, arthropods, and small mammals on the basis of surface temperature-controlled foraging times (Doyen and Tschinkel 1974, Wallwork 1982, Crawford 1991). Many small desert animals are weak burrowers, and soil surface microclimates are of great importance to their survival (Larmuth 1978).

Consequently, altering surface temperatures can affect nutrient availability and community structure for many desert organisms, thus increasing susceptibility to desertification.

Fire: High-intensity fire will burn biological crusts, resulting in reduction of visible cover, biomass, and species diversity (Callison et al. 1985, Greene et al. 1990, Johansen 1993). The extent of damage depends on the type of plant community in which the crust occurs, the distribution of fuel, and thus fire intensities (Johansen 1993). Exotic annual grasses, primarily *Bromus* spp., have invaded semiarid and arid landscapes throughout western North America, homogenizing fuel distribution and drastically altering fire regimes (Whisenant 1990). Increases in both fuel amount and continuity have resulted in large, continuous fires. Biological crusts are lost from the community if fire-return intervals are shorter than the period required for the crusts to recover (Greene et al. 1990, Whisenant 1990).

EXOTIC PLANTS

Introduced annuals such as cheatgrass and medusa-head wildrye (*Taeniatherum asperum*) appear to impose long-term threats to biological soil crust communities. Surveys in these plant communities show that the rich perennial moss/lichen community has generally been replaced with annual mosses and cyanobacteria. The mechanism by which the presence of annual grasses negatively affects the biological soil crusts is not clear but could include a decrease in available soil surfaces (via increased cover of vascular plant and plant litter), increased soil disturbance by small rodents responding to an increase in seed availability, increased fire frequency, increased soil turnover by increased populations of soil fauna, and/or increased soil disturbance by plant surface roots (Kaltenecker 1997).

RECOVERY FROM DISTURBANCE

Natural Recovery Rates

Species Composition: Recovery rates of biological soil crusts depend on the type and extent of disturbance and the availability of nearby inoculation material, as well as the temperature and moisture regimes that follow disturbance events. Recovery time is faster when crustal material is not removed, as pieces of remaining organisms are available to reinoculate recovering surfaces. Therefore, although most damage is done with the initial impact, recovery will be faster if disturbances are not repeated. Timing of the disturbance is also important. Damage is less severe when crusts are wet. In addition, if damage occurs when rain is imminent, then crustal organisms have an opportunity to reattach themselves before being blown away or buried. However, if disturbances occur before a long dry period, reattachment is not possible and much crustal material may be lost or too deeply buried for recovery. Size of disturbance can



be important, especially if crustal material has been lost from the disturbed site. As inoculant must come from adjoining areas, the size of the perimeter area relative to the internal surface area of the disturbance can heavily influence recovery rates (Belnap and Eldridge 2000). In addition, recovery is slower if soils in adjacent areas are destabilized. Sediments from these areas can either bury adjacent crusts, leading to their death, or provide material for “sandblasting” nearby surfaces, thus increasing erosion rates and slowing recovery (McKenna-Neumann et al. 1996).

Cyanobacteria or green algae recover first. *Microcoleus* is generally the first species to appear. Cyanobacteria are mobile and can often move up through disturbed sediments to reach needed light levels for photosynthesis, while slow-growing lichens and mosses are incapable of such movement. Instead, they require stable soil surfaces for growth, and colonization of these components generally takes place after surfaces have been stabilized by cyanobacteria. *Collema*, a nitrogen-fixing lichen, is generally the first lichen to appear.

The recovery process is more rapid in regions where soil surface moisture lasts for a longer period of time. Sites with fine-textured soils such as silt loams retain surface soil moisture for a longer period than do coarse-textured, sandy, or gravelly soils. Depending on all the above-mentioned factors, estimates of recovery time in cool deserts ranges from 14 to 35 years for cyanobacterial biomass, 45 to 85 years for lichen cover, and 20 to 250 years for moss cover (Belnap and Eldridge 2000).

Enhanced Recovery Rates

The use of inoculants to speed up recovery of crusts works well (Lewin 1977, Tidemann et al. 1980, Ashley and Rushforth 1984, St. Clair et al. 1986). In an experiment reported from southeast Utah, all measured responses were significantly enhanced by inoculation (Belnap 1993, 1995, 1996).

EVOLUTIONARY HISTORY OF DISTURBANCE

Soil and plant characteristics of most Intermountain ecosystems suggest that they probably evolved with low levels of soil surface disturbance by ungulates. These characteristics include limited surface water; sparse vegetation; the presence of biological soil crusts, which are easily disrupted by trampling; and the dependence of these ecosystems on nitrogen provided by the biological soil crusts (Evans and Ehleringer 1993, Evans and Belnap 1999). Dung beetles, present globally in other systems with large ungulate populations, are lacking (Mack and Thompson 1982). Limited surface water would have kept ungulate populations small and generally limited to winter use of lower elevations, as is seen today (Parmenter and Van Devender 1995). Winter use results in lower impacts to biological crusts (Marble and Harper 1989), as soils are wet or soon to be wet. Bunchgrasses that

lack adaptations to grazing such as tillering, secondary compounds, or high tissue silica content are dominant (Martin 1975, Stebbins 1981, Mack and Thompson 1982). In addition, shallow soils and low precipitation limit the distribution of burrowing vertebrate and invertebrate species. Thus, these systems may depend more heavily than other regions on soil surface integrity for natural ecosystem functioning. As a result, these deserts may be more negatively affected by soil surface disturbances than deserts that evolved with higher levels of surface disturbance.

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